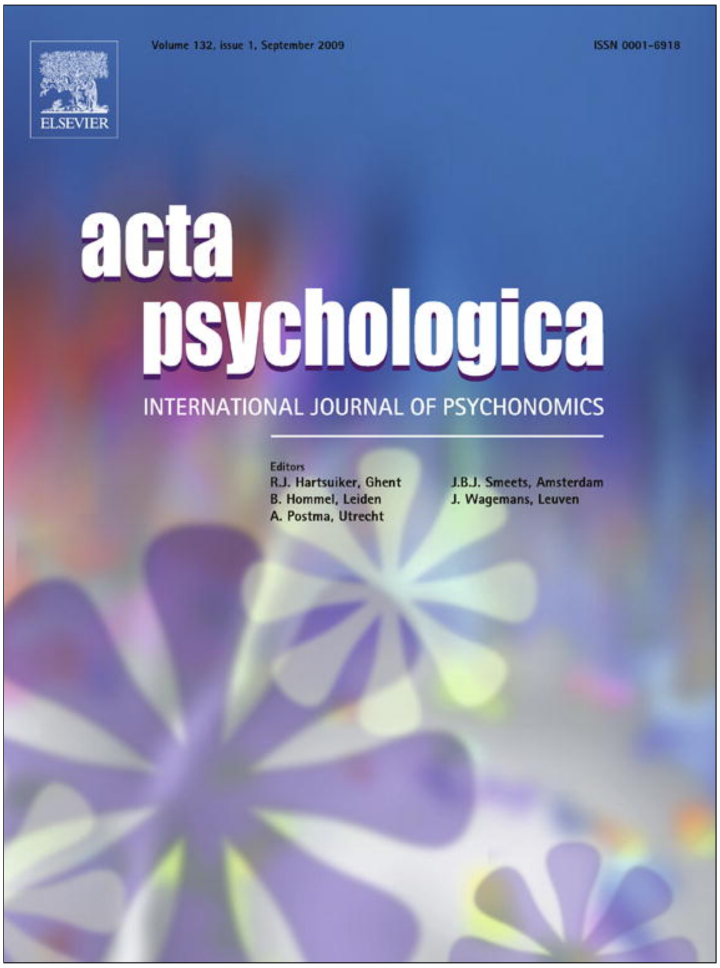
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A counterchange mechanism for the perception of motion

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ABSTRACT

A computational model for the perception of counterchange-specified motion is examined in detail and compared with various versions of the Reichardt motion detection model [Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In W. A. Rosenblith (Ed.), *Sensory communication* (pp. 303–317). New York: Wiley]. The counterchange model is composed of a pair of temporally biphasic subunits at two retinal locations, one detecting decreases and the other increases in input activation. Motion is signaled when both subunits are simultaneously excited, as determined by the multiplicative combination of their transient responses. In contrast with the Reichardt detector, which effectively tracks motion energy and accounts solely for results obtained with standard apparent motion stimuli (a surface is visible at one location, then at another), the counterchange model also accounts for the generalized apparent motion perceived between pairs of simultaneously visible surfaces. This indicates that standard apparent motion can be perceived via the same non-sequential, non-motion-energy mechanism as generalized apparent motion. There is no need for either an explicit delay mechanism to account for optimal motion perception at non-zero inter-stimulus intervals, or for inhibitory interaction between subunits to account for the absence of motion in the detector's null direction (Barlow, H. B., & Levick, W. R., 1965). Both are emergent properties that result from the inhibitory states of the counterchange detector's biphasic subunits. In addition to apparent motion, the counterchange principle potentially accounts for the perception of motion for drifting gratings, the short range motion perceived for random-dot cinematograms, and the motion perceived for continuously moving objects.

1. Introduction

When an object moves continuously across a darker background ("real" motion; Fig. 1a), or when it first appears in one location and is then discontinuously displaced to another location (apparent motion; Fig. 1b), there are multiple sources of visual information that could be the basis for the perception of its motion. There are sequential changes in position (Kinchla & Allan, 1969), there is motion energy due to spatiotemporal changes in luminance (Adelson & Bergen, 1985), and there is counterchange (discontinuous decreases in luminance at the location that was just occupied by the object, and discontinuous increases in luminance at its newly occupied location) (Hock, Gilroy, & Harnett, 2002).

However, it has been shown for pairs of simultaneously visible surfaces that neither the detection of sequential changes in position (Gilroy & Hock, in press; Hock, Kogan, & Espinoza, 1997; Lappin, Tadin, & Whittier, 2002), nor the detection of 1st- or 2nd-order motion energy (Gilroy & Hock, 2004; Hock & Gilroy, 2005; Hock et al., 2002) is necessary for the perception of apparent motion. It was found instead that it depends on the detection of counterchange (referred to as a dipole change by Lappin et al. 2002), a spatial pattern of oppositely signed changes in luminance or texture contrast. Motion begins at a surface where the change in luminance or texture contrast is *Toward* the background, and ends at a surface where the change is *Away* from the background (Fig. 1c and d). Because motion is perceived even when luminance changes for one surface and texture contrast changes for the other, as shown in Fig. 1e, it was concluded that it is more generally counterchanging activation that is the basis for the single-element apparent motion perceived between pairs of simultaneously visible surfaces; i.e., motion begins where activation decreases and ends where it increases, regardless of the stimulus changes responsible for the changes in activation (Hock & Gilroy, 2005).

The purpose of this article was to further validate the counterchange principle for the perception of motion by developing a computational model for the detection of counterchanging activation that accounts for the apparent motion perceived for a wide

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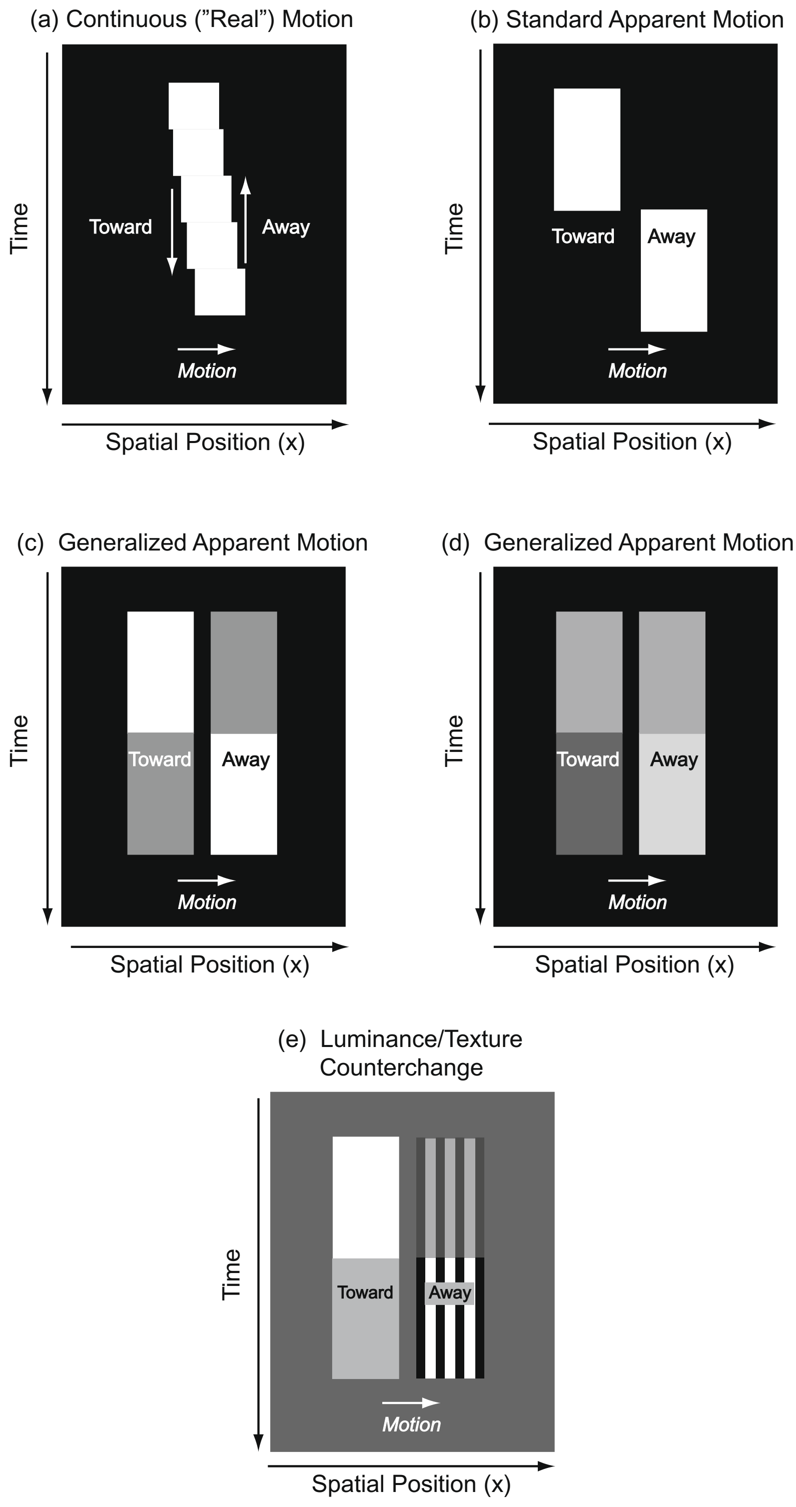

Fig. 1. Graphical representations of the discontinuous, oppositely signed changes produced by (a) a continuously moving object, (b) a standard apparent motion stimulus, (c, d) generalized apparent motion stimuli, and (e) a stimulus for which there is a change in luminance contrast for one surface and a change in texture contrast for another surface.

variety of stimuli, and potentially accounts as well for the motion perceived for drifting sine gratings, the short range motion perceived for random-dot cinematograms, and the motion perceived for continuously moving objects. It was anticipated that the detection of counterchange at pairs of spatial locations will prove to be the motion-detecting mechanism for 3rd-order motion, and thus complement 1st- and 2nd-order motion-energy mechanisms (Sperling & Lu, 1998).

The counterchange model, which was first proposed by Hock et al. (2002), incorporates pairs of subunits that respond transiently to oppositely signed changes in their input, one to decreases and the other to increases in input activation. As in other motion detection models (e.g., (Adelson & Bergen, 1985; Bischof & Di Lollo, 1996)), the transient responses are created by temporally biphasic detectors. Neurophysiological evidence for biphasic response to luminance change has been reported for neurons in both the lateral geniculate nucleus and cortex of the cat (Cai, DeAngelis, & Freeman, 1997; DeAngelis, Ohzawa, & Freeman, 1995). The biphasic subunits in the counterchange model that are excited by increased input activation and inhibited by decreased input activation could be composed of "nonlagged" cells; their response to light *in*crements is initially excitatory, then inhibitory (Humphrey & Weller, 1988; Mastronarde, 1987). The biphasic subunits in the counterchange model which are excited by decreased input activation and inhibited by increased input activation could be composed of "lagged" cells; their response to light *de*crements is initially excitatory, then inhibitory (Humphrey & Weller, 1988; Mastronarde, 1987).

Simulations are compared for the counterchange and Reichardt (1961) motion detector models. Although other motion detector models might plausibly be compared with the counterchange model, the Reichardt model was chosen because of the features it shares with the counterchange model, because it accounts for a wide range of apparent motion phenomena (Mather, 1990), and because it responds to local motion energy (van Santen & Sperling, 1985).

2. Implementation of the counterchange motion detector

The counterchange model is illustrated in Fig. 2. Like the Reichardt model, it multiplicatively combines the excitation of two spatially separated subunits; they must be simultaneously excited in order for motion to be perceived. Unlike the Reichardt model, the counterchange model responds to oppositely signed changes in input activation, and there is no explicit mechanism for delaying the excitation of one subunit prior to its multiplicative combination with the excitation of the other. Because the response of each subunit is transient rather than sustained, the counterchange model need not incorporate the Reichardt formulation's subtractive comparison of motion signals in opposite directions in order to avoid motion being signaled by static stimuli.

2.1. Biphasic subunits

The response kernels for the biphasic subunits give positive weight to recent inputs and negative weight to older inputs. The weights are balanced so that there is no response to constant input (the temporal frequency response is bandpass). 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). Temporal integration of each subunit's excitatory and inhibitory response is achieved through the convolution of the

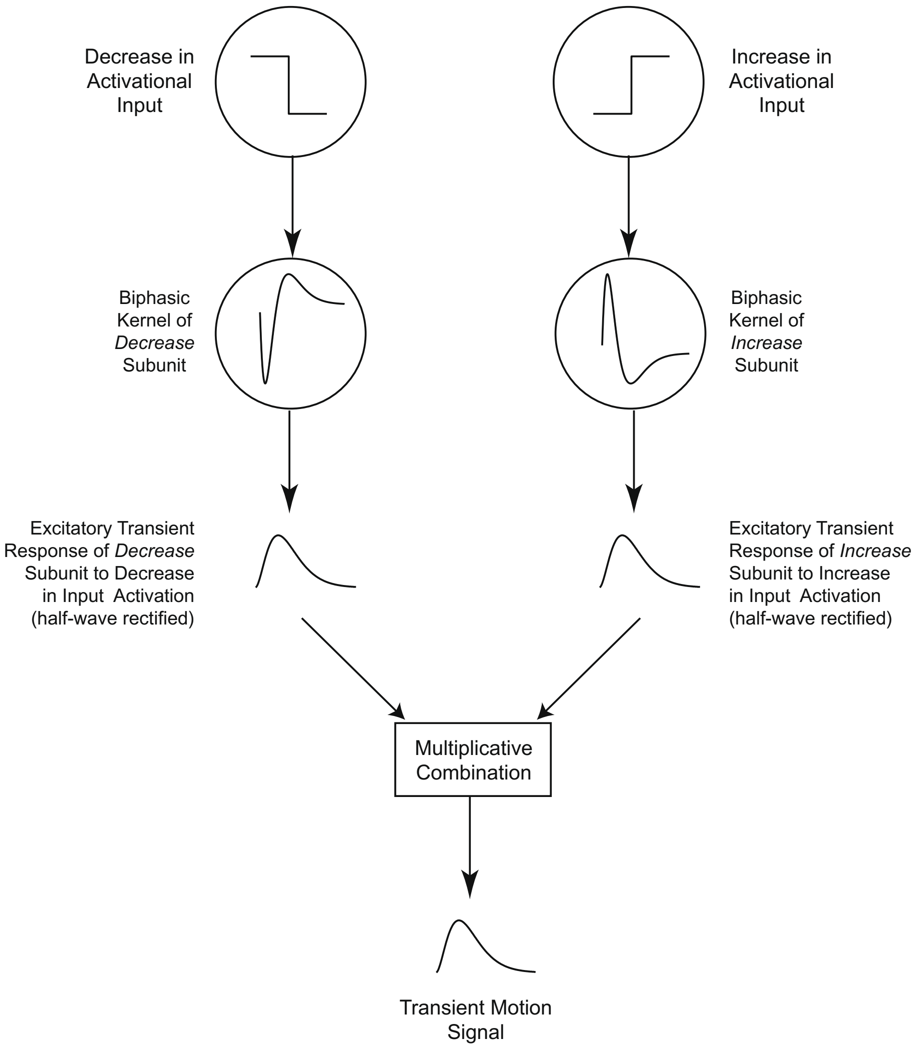

Fig. 2. Description of the counterchange motion detection mechanism.

biphasic subunit's response kernel with its time-varying activational input. The outputs of the two subunits are then half-wave rectified; i.e., only positive activation values are passed forward for multiplication.

Biphasic detectors create transient responses, so their product is also transient. The strength of motion detector activation is determined by the maximum of the motion detector's transient response. Motion is signified when post-multiplication activation rises from the detector's no-stimulus state (i.e., resting level), which has a negative value in the model, and crosses the threshold for perception, which is set at 0. The likelihood that motion will be perceived is assumed to depend on the extent to which the perceptual threshold is exceeded. (The latter implies that the motion signal is noisy. The more that the stimulus-determined motion detector activation exceeds the noise, the more likely it is that motion perception will be signified.)

2.2. Subunit asymmetry

Borst and Egelhaaf (1989) have pointed out that asymmetry in the responsiveness of pairs of subunits is an essential property for correlational models of motion detection (i.e., models in which subunit excitations are multiplicatively combined). The asymmetry introduced in the counterchange model is that the "Increase" subunit has a lower, no-stimulus resting level compared with the "Decrease" subunit. Consequently, larger changes in input activation are required for the "Increase" subunit to be excited compared with the "Decrease" subunit.[1]

2.3. Computations

The temporal evolution of activation was implemented with the dynamical equations that are given in the Appendix. Also given in the Appendix are parameter values for the biphasic subunits (each generates transient responses lasting as long as 325 ms), the no-stimulus resting levels of the biphasic subunits, and the post-multiplication resting level of the motion detector's output (the model takes the square root of the multiplied activation levels in order to prevent the activation of the motion detector from soaring). *The model's parameters were the same for all the simulations in this study*, including simulations for both generalized and standard apparent motion. Only the magnitude of the input activation varied from one simulation to the next. These variations reflected differences between generalized and standard apparent motion stimuli, and between short and long motion paths. The activational input could equivalently come from changes in 1st-order (luminance) or 2nd-order (contrast) information.

2.4. Spatial filters

The temporal dynamics of the counterchange model which are evaluated in this article are neutral with respect to the spatial filters that provide input to its biphasic "Decrease" and "Increase" subunits (i.e., spatial prefiltering; Morgan, 1992). It is assumed that pairs of spatial filters with a range of configurations, sizes, and spacing could provide this input, depending on the particulars of the motion stimulus. For the computational modeling that follows, it suffices to assume that the spatial filters are center/surround units that respond to changes in background-relative luminance contrast. Elongated spatial filters with one excitatory and one inhibitory lobe (i.e., edge detectors) are introduced later in the article in order to show that the counterchange model can account for motion phenomena other than apparent motion.

3. Implementation of the Reichardt motion detector

There are a number of different formulations of the Reichardt motion detector, all of which are composed of pairs of spatially separate subunits, with the activation of one subunit delayed prior to its comparison with the activation of the other (Borst & Egelhaaf, 1989; Reichardt, 1961; Reichardt & Egelhaaf, 1988). The delay, which is associated with the subunit that would be stimulated first by motion in the detector's preferred direction, brings the activation of the two subunits into temporal coincidence prior to their multiplication. The possibility of motion being signaled by static stimuli is avoided by subtracting the responses of two subunit pairs, one pair preferring motion in the opposite direction to the other.

In its simplest form, the Reichardt detector's subunits take the luminance values of the stimulus and carry them, with appropriate delay, to the multiplicative comparison stage (it could equivalently take contrast with the background as its input). The delay is implemented by lowpass temporal filtering for the first subunit that would be excited by motion in the detector's preferred direction. In our simulations, the delay is provided by a short-term memory-buffer, and abrupt changes in input to both subunits are smoothed by lowpass temporal filtering. The parameters for the low pass filters are the same as for the biphasic (bandpass) subunits, but without their inhibitory phase, so the subunits of the Reichardt detector are monophasic. As for the counterchange detector, it is assumed that there is a range of configurations, sizes, and spacing available for the spatial filters that provide input to the subunits of the Reichardt motion detector.

3.1. Alternative versions of the Reichardt motion detector

Reichardt detector (lowpass filters with different time constants). In this early version of the Reichardt model both subunits have lowpass temporal filters, but with different time constants (Hassenstein & Reichardt, 1956). Instead of a memory-buffer to provide a "pure" delay, a relative delay for the two subunits is introduced by having the longer time constant associated with the subunit that would be the first to be excited if motion were in the detector's preferred direction. Although this version of the model accounted for results obtained with standard apparent motion stimuli, its predictions for generalized apparent motion stimuli were more discrepant from experimental results than the version described above.

Reichardt detector (*biphasic filters*). In contrast with the lowpass temporal filtering in the original Reichardt model, other investigators have examined versions of the model in which the input is bandpass filtered, resulting in transient rather than sustained responses to changes in stimulation. This can be implemented with a pair of biphasic subunits that respond to same-signed changes in input activation (i.e., pairs of "Increase" or pairs of "Decrease" detectors). In one version, the two biphasic subunits have the same temporal characteristics, and a "pure" memory-buffer delay of the activational response of the initially stimulated subunit precedes its multiplicative combination with the activational

[1] Similar results were obtained for simulations based on the counterchange model when the gain was asymmetrical (more excitation of the "Decrease" than the "Increase" subunit for equal changes in input activation), and when there was asymmetrical interaction between the subunits (excitation of the "Decrease" subunit inhibits the "increase" subunit, but not vice versa). The counterchange model is therefore realizable with several different asymmetries, though not temporal asymmetries. That is, for either a delay in the response of the "Decrease" subunit prior to its multiplicative combination with the response of the "Increase" subunit, or a slower time constant for the "Decrease" than the "Increase" subunit, the motion signified by the model was optimal at non-zero inter-change intervals (ICIs) for the stimuli tested in Gilroy and Hock's (in press) first experiment. This was contrary to the results of the experiment (see Simulation 1).

response of a subsequently stimulated subunit (Bischof & Di Lollo, 1995). In another version the two bandpass (biphasic) temporal filters have different time constants and there is no memory-buffer to provide a "pure" delay (Baker & Cynader, 1994). Consistent with proposals by a number of investigators (e.g., Kahneman, 1967; Kolers, 1972; Lakatos & Shepard, 1997), biphasic versions of the Reichardt model treat apparent motion as depending on the detection of stimulus onset (or offset) asynchrony at two spatial locations.

Biphasic/transient versions of the Reichardt detector are generally successful in accounting for the perception of standard apparent motion. However, because they respond to same-signed changes in input activation, they do not signal motion for oppositely signed changes (i.e., a decrease combined with an increase in input activation) that result in the perception of motion for generalized apparent motion stimuli. However, numerous experiments beginning with Hock et al. (2002) have determined that motion is perceived for such stimuli. Moreover, the biphasic/transient versions of the Reichardt model signal motion for a pair of events that produces sequential increases in input activation at two locations, and for a pair of events that produces sequential decreases in input activation at two locations. In these cases, however, motion is not perceived (Gilroy & Hock, in press).

Reichardt detector (lowpass combined with bandpass filter). Baker and Cynader (1994) and Bischof and Di Lollo (1996) have examined a version of the Reichardt model in which one subunit responds monophasically (sustained response) and the other biphasically (transient response), without a "pure" delay. However, the model incorrectly predicts that motion will be perceived for the very simple case in which one surface is continuously present (sustained response), and the second surface suddenly appears or disappears at another location (transient response).

4. Simulations: counterchange, sequence, and motion energy

Both the counterchange and Reichardt models account for a wide range of motion phenomena for standard apparent motion stimuli (a surface appears at one location, then is discontinuously shifted to another location). Where the Reichardt model falls short is in accounting for the temporal dynamics of motion perception for generalized apparent motion stimuli (motion is perceived between two simultaneously visible surfaces as a result of changes in the luminance of the surfaces).

Simulations of experimental results for generalized apparent motion stimuli are included in this section which indicate that (1) motion is perceived from the surface for which there is a *Toward* change in background-relative luminance contrast to a surface for which there is an *Away* change in background-relative luminance contrast, even when the two events occur in reverse temporal order (i.e., the *Away* change precedes the *Toward* change), and (2) motion is not perceived for either a sequence of equal-sized *Away* changes, or simultaneous but unequal *Away* changes for the two surfaces, despite the presence of motion energy.

4.1. Simulation 1: sequences of Toward and Away changes

Experiment 1 in Gilroy and Hock (in press) provided evidence that the perception of generalized apparent motion depends on the detection of oppositely signed rather than on same-signed stimulus events occurring at different spatial locations, regardless of whether the stimulus events are simultaneous or sequential. Motion was perceived when a *Toward* change was presented before, after, or simultaneously with an *Away* change (Fig. 3a and b). The stimuli were from Experiment 1a of Gilroy and Hock (in press). The two surfaces were present for two sec before the first change in luminance contrast and removed two sec after the second change in luminance contrast, so changes in input activation at the start and end of each trial were of no consequence for motion perception.

Counterchange model. For both experiment and simulation (Fig. 3c and d), motion was perceived from the location with decreased input activation to the location with increased input activation, regardless of the order of the *Toward* and *Away* changes creating these activation changes, and was perceived for longer inter-change intervals (ICIs) when the *Toward* preceded the *Away* change than vice versa.

Single trial simulations showing how activation evolves over time are presented in Fig. 4. When the ICI is 50 ms, motion is signified regardless of the temporal order of the stimulus changes and the level of motion detector activation is somewhat greater in the *Toward*-before-*Away* than the *Away*-before-*Toward* condition (Fig. 4a and b), both consistent with the experimental results. Motion is also signified when the *Toward* change precedes the *Away* change by 215 ms, but not vice versa. The latter is the case because the low, negative resting level for the "Increase" subunit results in the excitatory states of the two subunits not overlapping in time (Fig. 4c).

Reichardt model. Simulations correctly signal motion direction, but contrary to experiment, predict an advantage for motion perception in the *Away*-before-*Toward* condition compared with the *Toward*-before-*Away* condition (Fig. 3e).

4.2. Simulation 2: sequences of away changes

Instructions to participants in Experiment 1 of Gilroy and Hock (in press) minimized the possibility of attentive tracking (Cavanagh, 1992), so motion was not perceived for trials with successive *Away* changes (or successive *Toward* changes) in luminance contrast, first at one location then at the other, regardless of the time between the changes (Fig. 5a). This was correctly predicted by the counterchange model, which requires oppositely signed changes in input activation in order for motion to be perceived. However, both rightward and leftward motions were incorrectly signaled for this stimulus by the Reichardt model, even for very long time intervals between the luminance increments (Fig. 5c). The Reichardt model effectively tracks motion energy. It signaled leftward motion when there was an increase in the luminance of the left-hand surface that shifted the centroid of the luminance profile to the left, and then signaled rightward motion when there was an increase in the luminance of the right-hand surface that shifted the centroid back to the midpoint between the two surfaces (Fig. 5b). The simulation therefore confirmed experimental evidence indicating that the detection of motion energy is not required for the perception of single-element apparent motion. This was also the case for the simulation that follows:

4.3. Simulation 3: motion energy without counterchange

Hock et al. (2002) showed that the presence of motion energy is not sufficient for single-element motion to be perceived between two simultaneously visible surfaces undergoing simultaneous changes in luminance contrast. They tested stimuli with and without counterchange (Fig. 6a and b). For the latter Co-Change stimuli, luminance contrast was initially greater for one surface, but during the next frame, simultaneous but unequal increases resulted in luminance contrast becoming greater for the second surface. Motion was not perceived, despite the presence of the motion energy generated by this shift in the location with the higher luminance contrast.

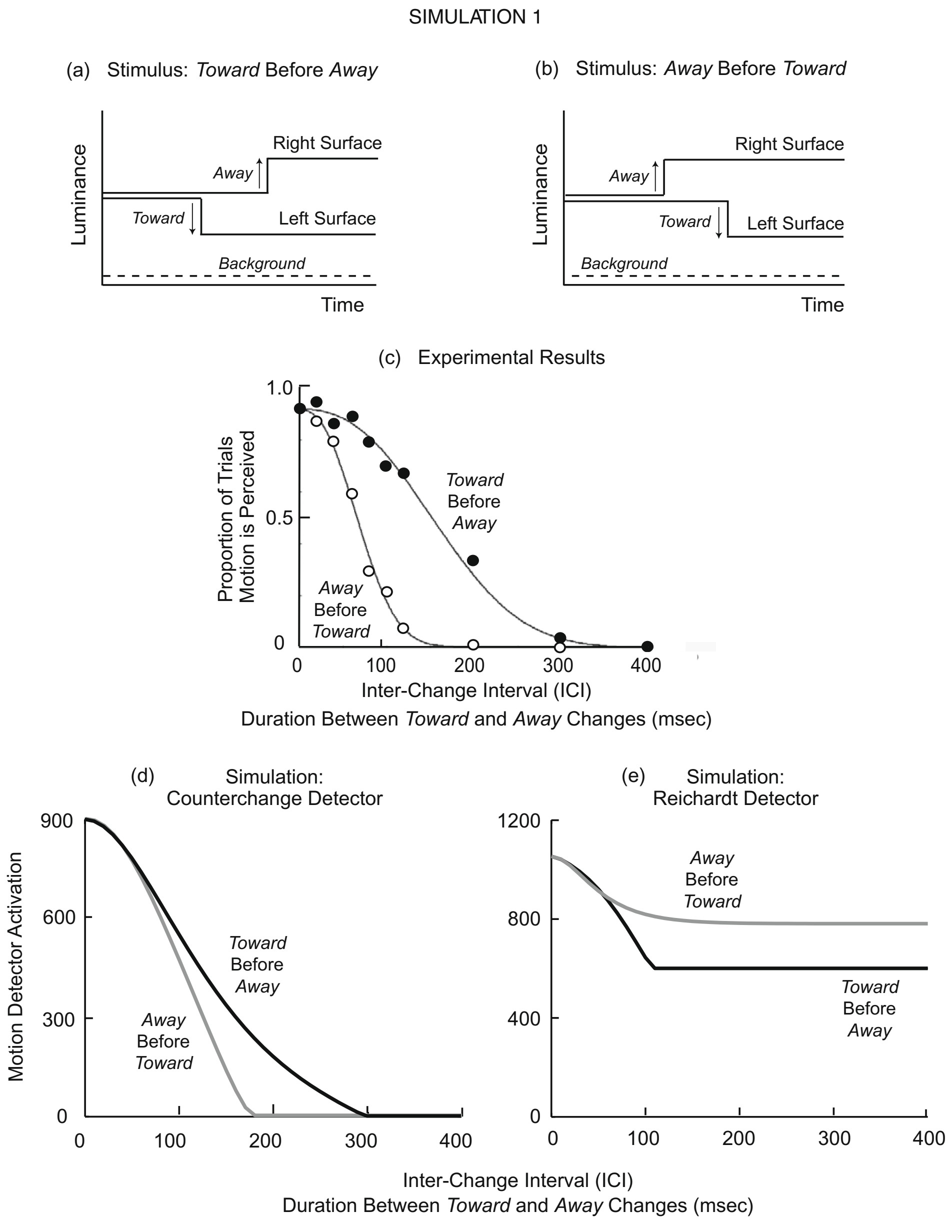

Fig. 3. Simulation 1. (a, b) Graphic examples of the *Toward*-before-*Away* and *Away*-before-*Toward* stimuli. Rightward motion is perceived for these stimuli regardless of the temporal order of the *Toward* and *Away* changes. (c) The proportion of trials in which motion is perceived as a function of the inter-change interval (ICI) in Experiment 1a of Gilroy and Hock (in press). The results are averaged over three participants. (d) Simulation of experimental results based on the counterchange model. (e) Simulation of experimental results based on the Reichardt model.

The background-relative luminance change (BRLC) of the surfaces was varied in this experiment,[2] and pairs of stimuli with and without counterchange were matched in motion energy content by integrating and comparing the energy within different quadrants of the Fourier-transformed space/time profiles. Motion was perceived only for the stimuli with counterchange (Fig. 6c). These results were well simulated by the counterchange model (Fig. 6d), but not by the Reichardt model (Fig. 6e). The Reichardt motion detector tracks motion energy, so it incorrectly signifies that motion would be perceived, irrespective of the presence or absence of counterchange.

[2] The background-relative luminance change (or BRLC) at each surface location was determined by dividing the luminance change for the surface by the difference between its average luminance and the luminance of its background (Hock et al., 1997).

5. Simulations: the biphasic detection of changes in luminance contrast

Experiments 3 and 4 in Gilroy and Hock (in press) provided psychophysical evidence that *Toward* and *Away* changes are detected by biphasic subunits. They did so by showing that excitatory responses to changes in luminance contrast can be reduced by inhibitory responses to preceding or following changes in luminance contrast. In Experiment 3, motion was perceived less frequently when the time between consecutive *Away* and *Toward* changes at the same location was brief (Fig. 7b), consistent with biphasic "Increase" subunits being excited by increased input activation (due to the *Away* changes), but having the growth in their activation "cut-off" by the inhibition produced by immediately following decreases in input activation (due to the *Toward* changes). In Experiment 4, motion was perceived less frequently when the time between consecutive *Toward* and *Away* changes at

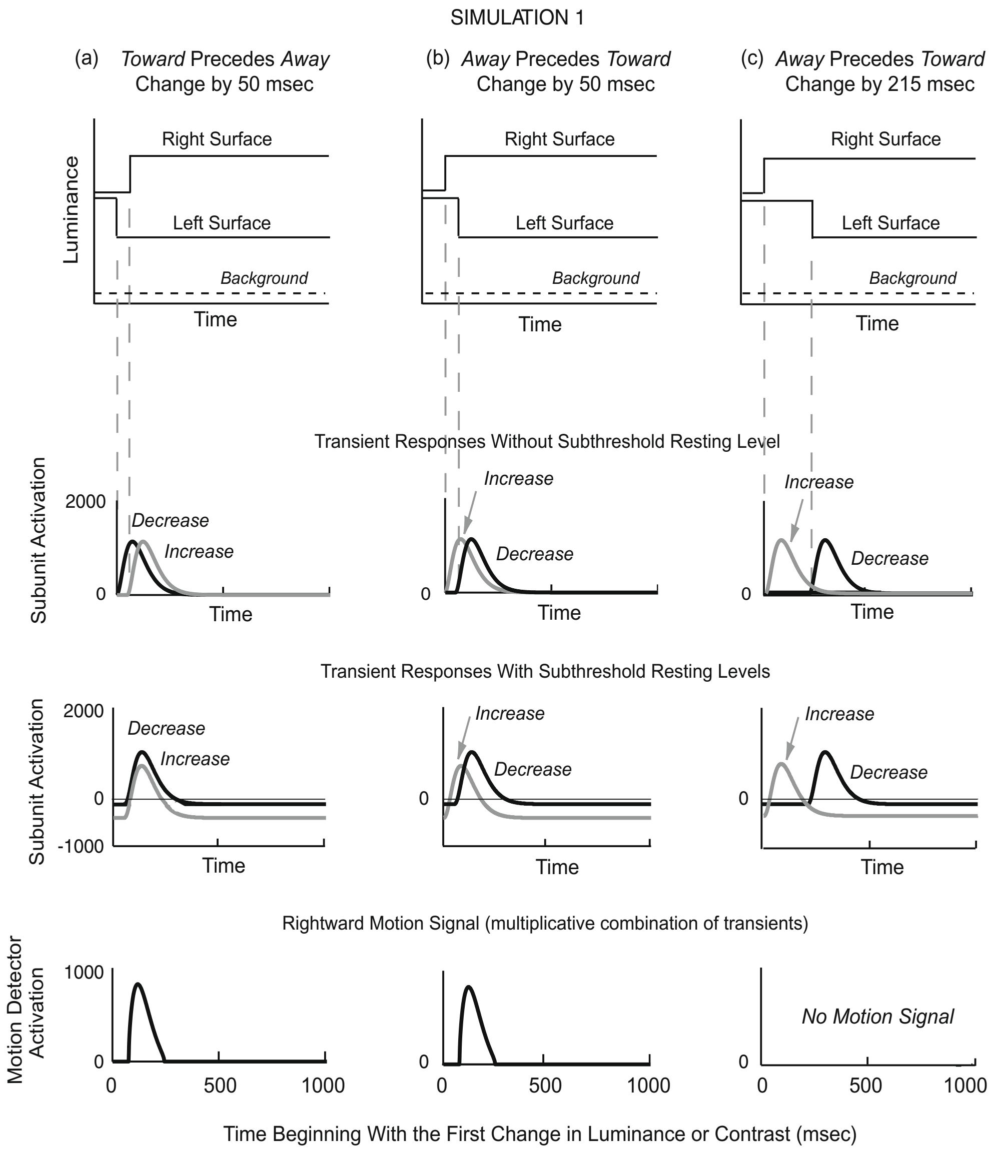

Fig. 4. Simulation 1. Single trial simulations based on the counterchange model when (a) *Toward* changes precede *Away* changes by 50 ms, (b) *Away* changes precede *Toward* changes by 50 ms, and (c) *Away* changes precede *Toward* changes by 215 ms. The simulations show the evolution of activation for the "Decrease" and "Increase" subunits, the effects of asymmetric resting levels on the activation levels of the "Decrease" and "Increase" subunits, and the motion signal resulting from the multiplicative combination of the latter subunit activations (following half-wave rectification).

the same location was brief (Fig. 7b), consistent with biphasic "Decrease" subunits being excited by decreased input activation (due to the *Toward* changes), but being inhibited by immediately preceding increases in input activation (due to the *Away* changes). The simulations follow:

5.1. Simulation 4: biphasic "increase" response inhibited by a subsequent toward change

In Experiment 3 of Gilroy and Hock (in press), the surface for which there had just been an *Away* change was removed, creating a *Toward* change a variable duration after the motion-specifying *Toward/Away* counterchange (Fig. 7a). Motion was perceived less frequently when the time between consecutive *Away* and *Toward* changes at the same location was brief (Fig. 7b). These results were well simulated by the counterchange model (Fig. 7c). In addition, it can be seen in Fig. 7e that the reduction in motion perception for brief durations between consecutive *Away* and *Toward* changes at the same location was due to the "cut-off" in the growth of the "Increase" subunit's excitatory response to the *Away* change by the inhibition caused by the subsequent *Toward* change.

The Reichardt model failed to simulate the results of the experiment (Fig. 7d). Although motion was perceived only in the rightward direction for the stimulus illustrated in Fig. 7a, both rightward and leftward motions are signified at different points in time during the same trial. Rightward motion energy is created relatively early in the trial by the simultaneous *Toward* and *Away* changes, and leftward motion energy is created later in the trial when the right-hand surface is removed.

5.2. Simulation 5: biphasic "decrease" response inhibited by a preceding away change

This experiment demonstrated that the detectability of a *Toward* change is reduced when it is immediately preceded by an *Away* change at the same location. As shown in Fig. 8a, the luminance contrast of the left-hand surface increases, creating an *Away* change a variable duration before the motion-specifying *Toward/*

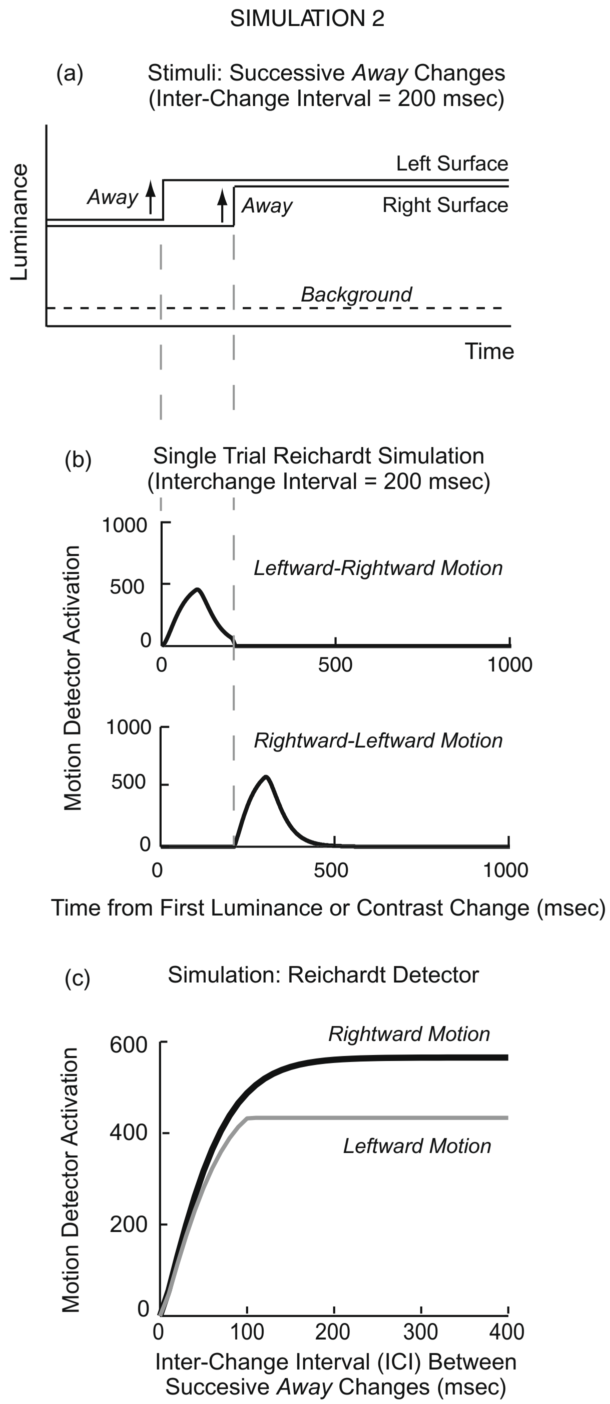

Fig. 5. Simulation 2. (a) Graphic examples of successive *Away* changes in luminance contrast at two locations. Motion is not perceived for these stimuli (Experiment 1a of Gilroy and Hock, in press). (b) Single trial simulation with an inter-change interval (ICI) of 200 ms showing that the Reichardt model signals motion in two directions for the same stimulus, though at different points in time. (c) Simulation based on the Reichardt model, which incorrectly predicts that motion will be perceived. (Nonmotion is signaled by the counterchange model.)

Away counterchange. Motion was perceived less frequently when the time between consecutive *Away* and *Toward* changes at the same location was brief (Fig. 8b). These results were well simulated by the counterchange model (Fig. 8c), but not by the Reichardt model (Fig. 8d). Both rightward motion and leftward motion were incorrectly signified by the Reichardt model at different times during the trial, consistent with shifts in the centroid of the stimulus' luminance profile (i.e., motion energy).

Of particular interest for the counterchange simulation is the response of the biphasic "Decrease" subunit (Fig. 8e). Its excitation is reduced for brief durations between *Away* and the *Toward* changes at the same location. This is because brief durations leave insufficient time for the "Decrease" subunit to recover from the inhibition produced by the preceding increase in input activation. As a result, the excitatory effect of the decrease in input activation begins while the "Decrease" subunit is still in an inhibitory state. As can be seen in Fig. 8e, recovery from inhibition is almost complete when the increase precedes the decrease in input activation by 250 ms, but recovery has not begun when the increase precedes the decrease in input activation by 50 ms.

6. Intermediate summary

6.1. Motion energy

Simulations based on the counterchange model always were consistent with the results obtained with generalized apparent motion stimuli. This was not the case for simulations based on the Reichardt model, which predicted motion on the basis of the motion energy in the stimulus, even when the counterchange model predicted otherwise. Thus, the Reichardt model incorrectly predicted that motion would be perceived for pairs of simultaneously visible surfaces when there was a succession of equal increases in luminance contrast for the two surfaces (Simulation 2), when there was a simultaneous but unequal increase in luminance contrast such that the location of the surface with the higher contrast changed (Simulation 3), and when one of the two surfaces was removed (Simulation 4). Experimental evidence that single-element apparent motion between two spatial locations is not based on motion energy extraction was complemented by the results of these simulations.

6.2. Sequential information

Although the Reichardt detector presumably is designed for the detection of sequential visual events (the response of one subunit is delayed in order to bring its activation into alignment with that of a subsequently stimulated subunit), in contrast with the counterchange model it does not account for how the sequential order of *Toward* and *Away* changes affects the perception of generalized apparent motion (Simulation 1). The applicability of the Reichardt model to the generalized apparent motion was not improved by varying the model's temporal parameters, and it is unlikely that its "elaborated" version (van Santen & Sperling, 1985) would fare better.

6.3. Biphasic inhibition

The key discovery from the simulations reported thus far is the importance of biphasic inhibition for understanding the temporal dynamics of motion perception. The effects of biphasic inhibition are further addressed in the section that follows. The simulations will be for experiments with standard, two-flash apparent motion, a special case of generalized apparent motion for which the lower luminance value of each surface equals the luminance of the background during alternate frames. Because a surface appears at one location, then disappears and re-appears at another, sequential position information is available in addition to counterchanging luminance contrast. The simulations will show that the counterchange model accounts for two-flash apparent motion perception despite the presence of phenomenologically salient position

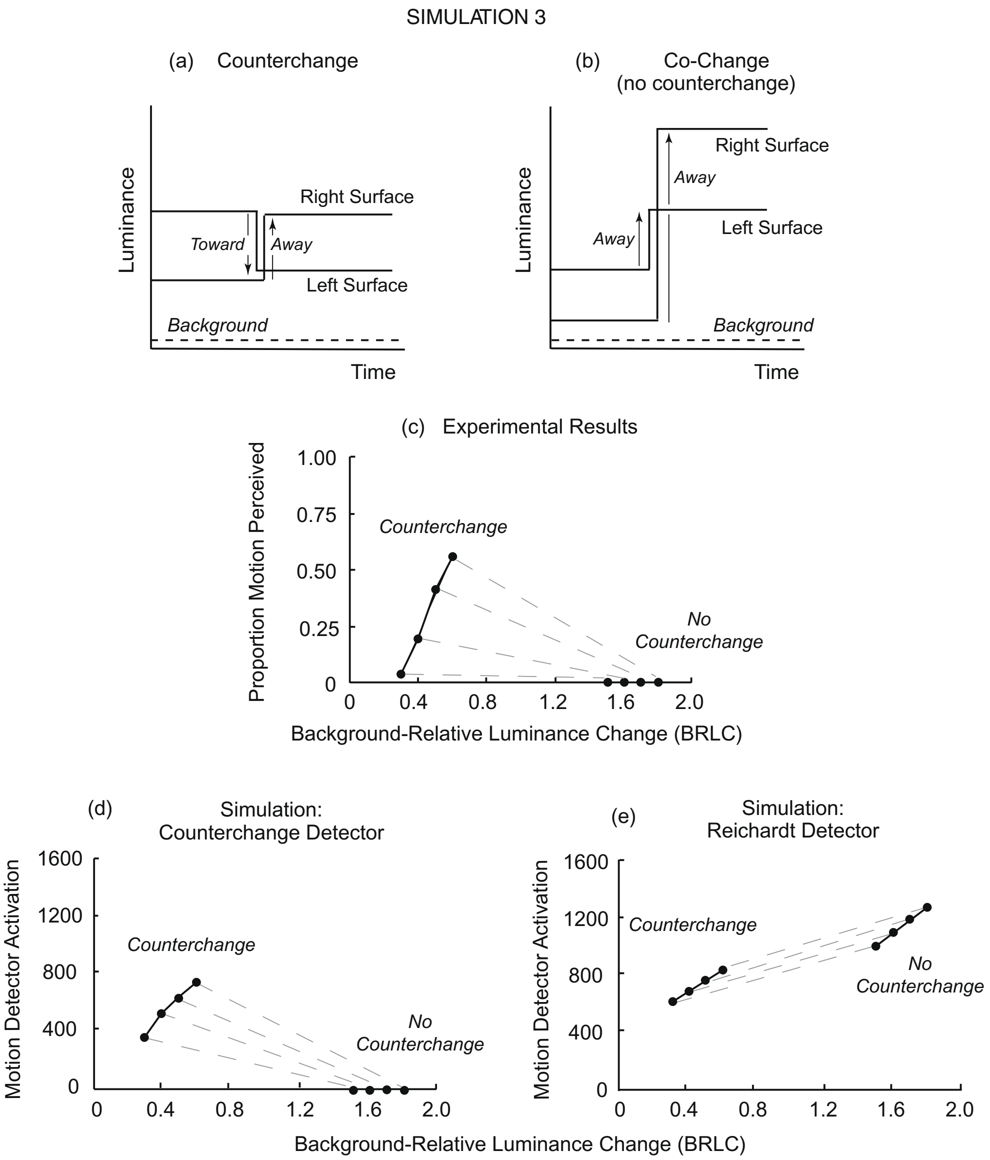

Fig. 6. Simulation 3. Graphic examples of the luminance contrast changes for (a) the Counterchange condition, and (b) the Co-Change condition (no counterchange) in Experiment 1 of Hock et al. (2002). Motion is perceived only for the stimuli with counterchange. (c) The proportion of trials motion is perceived (averaged over the three participants) as a function of the background-relative luminance change (BRLC) for the right-hand surface (the BRLC value always was 0.6 for the left-hand surface). The pairs of Counterchange and Co-Change stimuli that are matched in motion energy content (see text) are connected by broken lines. (d) Simulation of experimental results based on the counterchange model. (e) Simulation of experimental results based on the Reichardt model.

information. Simulations based on the Reichardt model, which were generally consistent with the results for standard apparent motion, are not presented.

7. Simulations: biphasic inhibition and two-flash apparent motion

Each flash of a standard, two-flash apparent motion stimulus is composed of a luminance onset (*Away* change) followed by its offset (*Toward* change). Counterchange-specified motion perception depends on the *Toward* change due to the offset of the first flash in combination with the *Away* change due to the onset of the second flash (Fig. 9a). Whether or not motion is perceived for two-flash apparent motion stimuli depends on the durations of the flashes and the inter-stimulus interval (ISI) between them.

7.1. Simulation 6: emergent delay – recovery from biphasic inhibition

For relatively brief flashes (frame durations), motion is optimally perceived for non-zero inter-stimulus intervals (ISIs) between the flashes. This is consistent with the delay that is an explicit feature of the Reichardt model, but can also be accounted for by the counterchange model on the basis of recovery from biphasic inhibition. As discussed with Simulation 5, biphasic inhibition arises when "Decrease" subunits are inhibited by increases in input activation. This inhibition, which occurs upon the onset of the first flash, is not passed forward to the multiplication phase of the model (each subunit's activation is half-wave rectified),

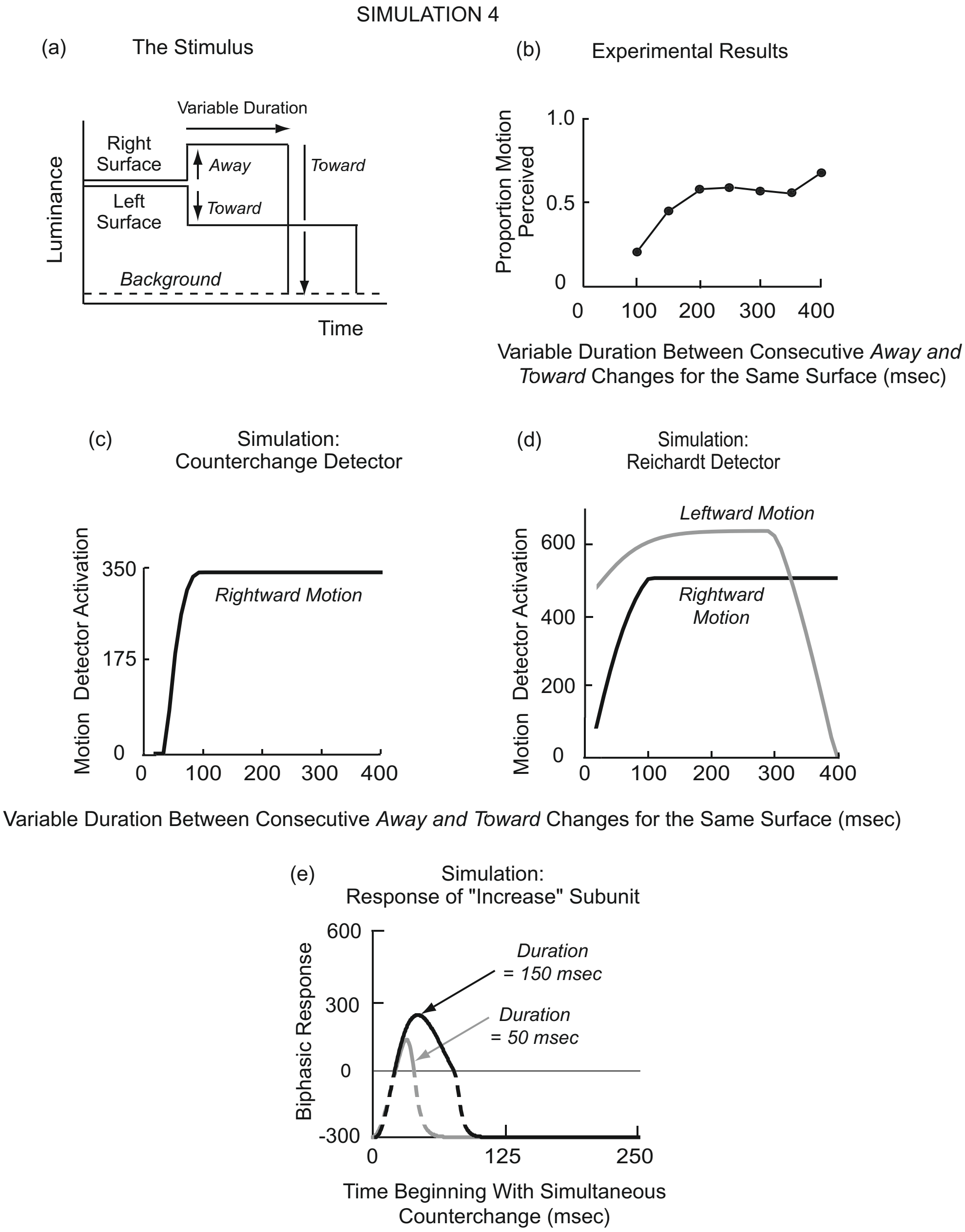

Fig. 7. Simulation 4. (a) Graphic examples of stimuli with consecutive *Away* and *Toward* changes at the same location (Experiment 3 of Gilroy and Hock (in press)). The *Toward* change occurs a variable interval after the motion-specifying *Toward/Away* counterchange. (b) The proportion of trials motion is perceived averaged over the two participants and the different BRLC values in the experiment. (c) Simulation of experimental results based on the counterchange model. (d) Simulation of experimental results based on the Reichardt model. (e) Simulated response of the "Increase" subunit as a function of the duration preceding the removal of the surface for which there had just been an increase in input activation. Levels of subunit activation below zero are not passed forward for multiplication with the activation of the "Decrease" subunit.

but it nonetheless delays and reduces the excitatory response of the "Decrease" subunit to the offset of the flash.

For brief flash durations (e.g., 20 ms), and an ISI of 0 ms, the delay required for recovery from biphasic inhibition is long enough for the excitatory phase of the "Decrease" response to occur after the excitatory phase of the "Increase" subunit has ended (Fig. 9b). In the absence of temporal overlap, motion is not signaled by the counterchange detector. However, the introduction of a non-zero ISI provides additional time for the recovery of the "Decrease" detector from biphasic inhibition. For the 20 ms frame duration, separating the two flashes by an ISI of 78 ms brings the excitatory peaks of the biphasic responses of the "Decrease" and "Increase" subunits into temporal alignment, and motion is optimally signified (Fig. 9c). When the flash duration is sufficiently long (300 ms in Fig. 9d), there is ample time for recovery from inhibition. The peaks of the "Decrease" and "Increase" excitatory responses are temporally aligned, so motion is optimally signified when the ISI is 0 ms, as observed by Gilroy and Hock (in press).

7.2. Simulation 7: Korte's 4th law (Korte, 1915)

The above effects of biphasic inhibition point to a trade-off between flash/frame duration and ISI; briefer frame durations require longer ISIs in order for motion to be optimally perceived (Korte's

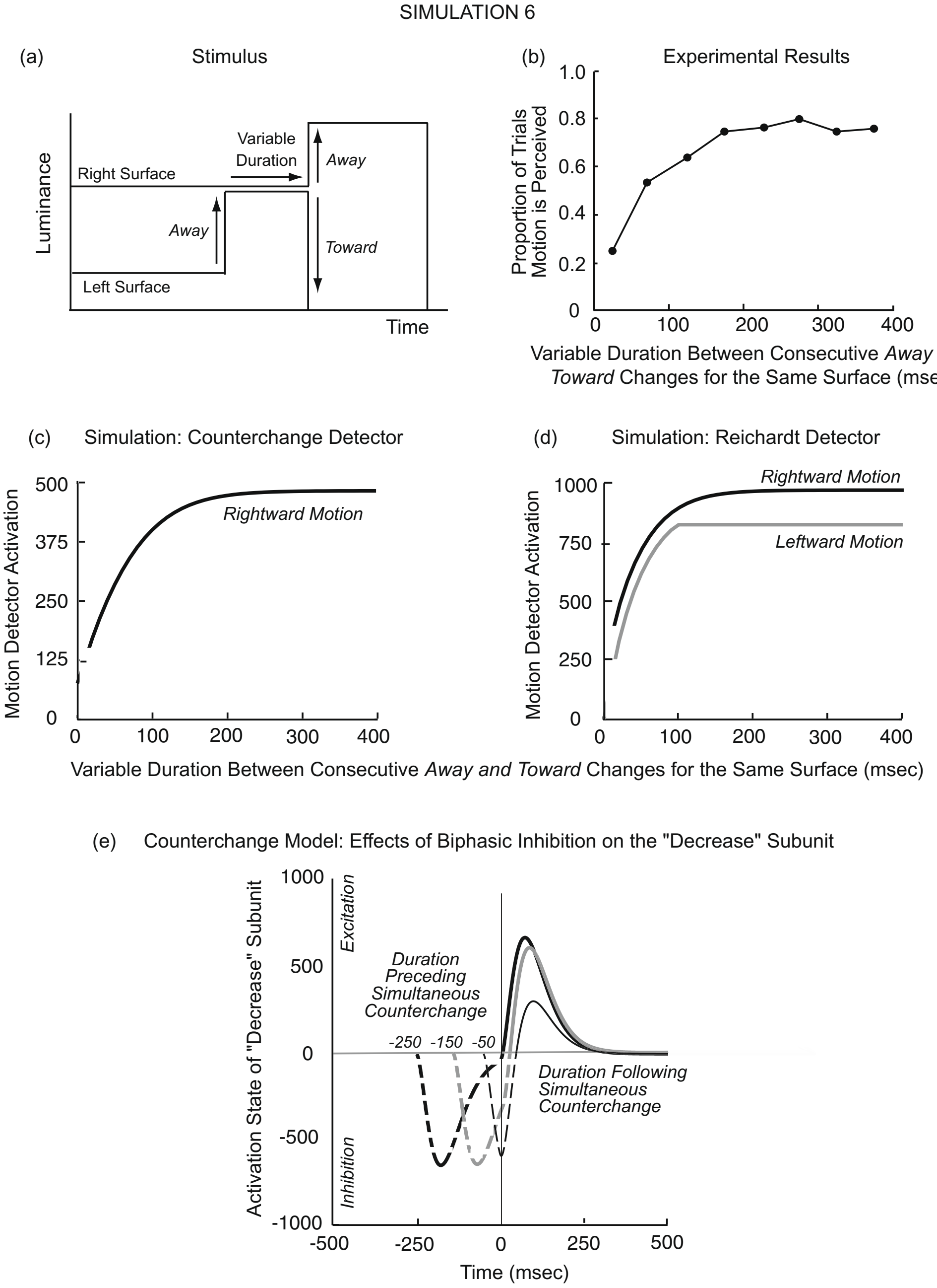

Fig. 8. Simulation 5. (a) Graphic examples of stimuli with consecutive *Away* and *Toward* changes at the same location (Experiment 4 of Gilroy and Hock (in press)). The *Away* change occurs a variable interval before the motion-specifying *Toward/Away* counterchange. (b) The proportion of trials motion is perceived, averaged over the two participants. (c) Simulation of experimental results based on the counterchange model. (d) Simulation of experimental results based on the Reichardt model. (e) Simulated responses of the "Decrease" subunit in the counterchange model graphed as a function of the duration that the decrease in input activation is preceded by the increase in input activation, the latter creating biphasic inhibition. Levels of subunit activation below zero are not passed forward for multiplication with the activation of the "Increase" subunit.

4th law). Kolers' (1964) results are generally consistent with this relationship, but his observers reported the quality of the perceived motion (whether it was continuously smooth) rather than whether it was perceived or not. We therefore supplemented his results with an experiment in which participants simply reported whether or not they perceived motion. As for Kolers' results, the frequency with which motion was perceived was an inverted-U-shaped function of ISI (Fig. 10a).

Our results and Kolers' are readily simulated by the counterchange model (Fig. 10b), with optimal motion signified at 78 ms when the flash/frame duration was 20 ms (as per Fig. 9c). This ISI value was close to the optimal ISI in our experiment and Kolers'. The inverted-U function reflects a combination of recovery from biphasic inhibition, which reduces motion perception for brief ISIs (Fig. 9b), and the limited duration of the "Decrease" and "Increase" transients, which eliminates motion perception for ISIs too long for the transients to temporally overlap (Figs. 3 and 4).

Sgro's (1963) observers indicated whether or not they perceived a single element in motion for a standard apparent motion stimulus. Fig. 10c combines his data obtained when frame duration was

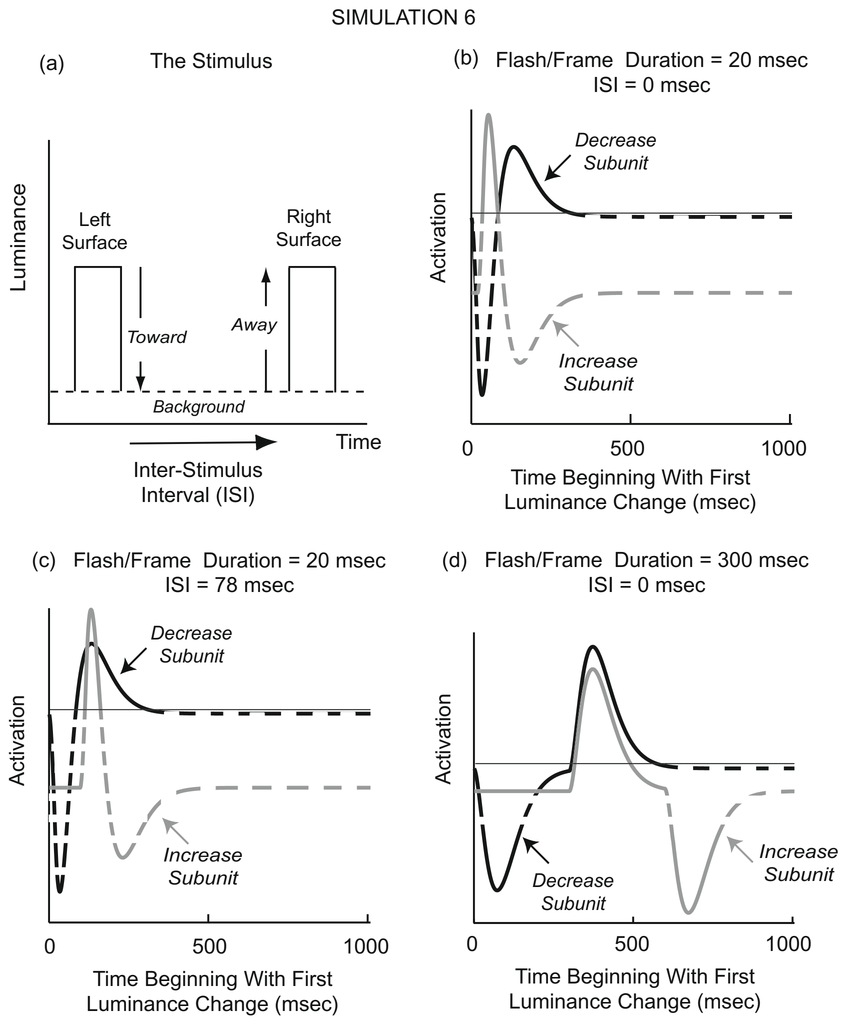

Fig. 9. Simulation 6. (a) A graphic example of a standard, two-flash apparent motion stimulus. (b–d) Responses of "Decrease" and "Increase" subunits for different combinations of flash/frame duration and inter-stimulus interval (ISI). Motion strength increases with increased temporal overlap between the "Decrease" and "Increase" transients. Levels of subunit activation below zero are not passed forward for multiplication.

held constant and ISI varied, and when ISI was held constant and frame duration varied. His results, which are consistent with Korte's 4th law, are well simulated by the counterchange model.

7.3. Simulation 8: Korte's 3rd law (Korte, 1915)

Korte's 3rd law specifies that longer ISIs are required for the perception of apparent motion over greater distances. Results generally consistent with this relationship were reported long ago by Neuhaus (1930). A re-formatted version of these data by Kolers (1972) is reproduced in Fig. 11b for flash durations of 10 ms. Neuhaus not only found that the minimum ISI required for apparent motion increases with spatial separation, but found as well that the perception of motion is lost when the ISI is too long, especially for larger spatial separations. The simulation of Neuhaus' (1930) results follows from the assumption that changes in the activational input to the counterchange motion detector decrease with increased spatial separation, possibly because sensitivity to luminance change decreases for the increasingly peripheral locations of surfaces when they are further and further apart (Tyler, 1987; Treutwein & Rentschler, 1992).

The key to the counterchange account of Korte's 3rd law is that the minimum ISI required for motion perception depends on spatial separation when presentation durations are relatively brief; i.e., when a portion of the ISI interval is required for recovery from biphasic inhibition (Simulation 6). As illustrated by the simulation shown in Fig. 11a, the minimal ISI required for the perception of apparent motion increases when increased spatial separation weakens the motion signal, as per the 3rd law (note the arrow on the left), and in addition, that the maximum ISI over which motion can be perceived decreases with increased spatial separation, as also occurs in Neuhaus' data (note the arrow on the right).[3] As can be seen in Fig. 11c, the counterchange model provides a qualitative simulation of Neuhaus' (1930) results.

7.4. Simulation 9: motion over long vs. short paths

Either diagonally rightward or diagonally leftward motion is perceived for Burt and Sperling's (1986) multi-frame apparent motion stimuli (Fig. 12a). Short path, diagonally rightward motion is most frequently perceived for relatively long ISIs, consistent with input activation being greater for the shorter motion paths, and consistent as well with long ISIs providing ample time for recovery

[3] Korte's 2nd law (Korte, 1915) specifies that there is an inverse relationship between inter-stimulus interval (ISI) and intensity; i.e., longer ISIs are required in order for motion to be perceived when changes in luminance contrast are smaller. The 2nd law follows from the simulation in Fig. 11a, with decreased luminance contrast replacing increased spatial separation in reducing the range of ISI values over which motion is signified by the counterchange model.

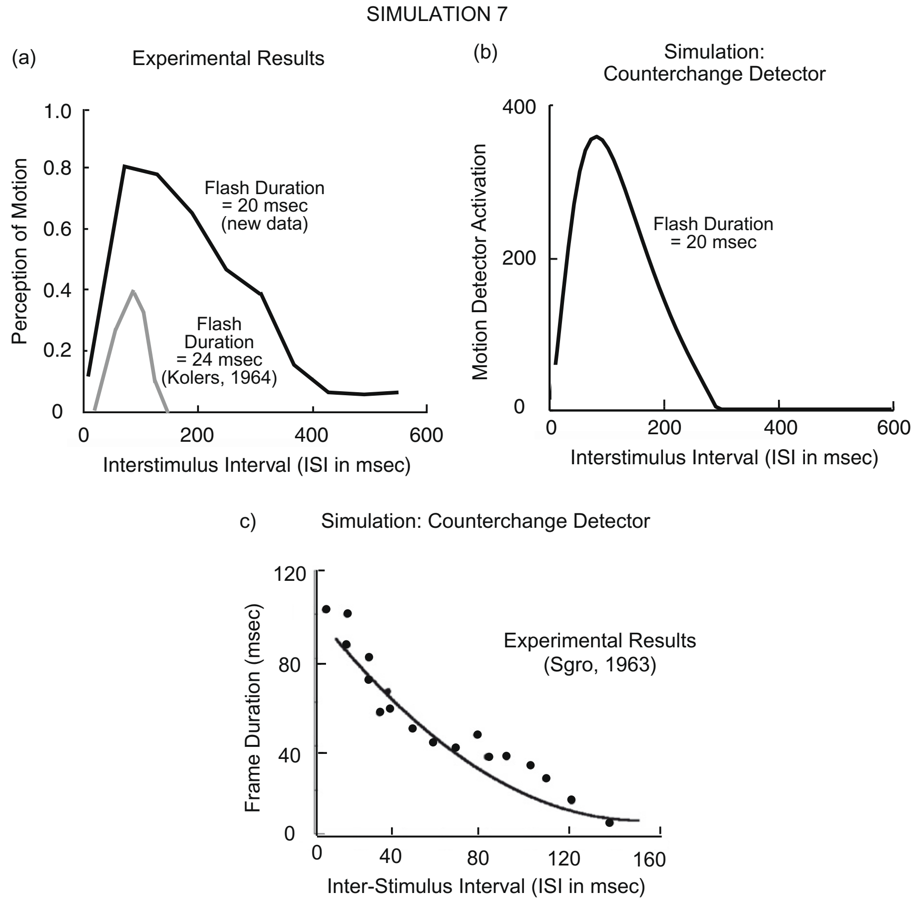

Fig. 10. Simulation 7. (a) Results from an experiment by Kolers (1964) for a flash/frame duration of 24 ms, and results obtained in our laboratory with different response criteria (the flash/frame duration was 20 ms). (b) Simulation based on the counterchange model for a flash/frame duration of 20 ms. (c) Compilation of results reported by Sgro (1963). The results of the counterchange simulation (solid line) are superimposed on his data.

of the biphasic "Decrease" subunits from inhibition resulting from the preceding onset of the dots. For brief ISIs, however, motion was more frequently perceived over the longer, diagonally leftward paths. This occurs because the long path motion is established over every other frame, effectively creating a longer temporal interval during which there could be recovery from biphasic inhibition. Burt and Sperling's (1981) results and their simulation by the counterchange model are presented in Fig. 12b and c.[4]

8. Counterchange vs. Reichardt motion detection

In this article we have developed a computational model of counterchange detection entailing the multiplicative combination of temporally biphasic (bandpass) responses to stimulus changes occurring at the two locations of an apparent motion stimulus. One biphasic subunit responds to stimulus changes creating decreases in input activation while the other responds to stimulus changes creating increases in input activation. Because the subunits of the counterchange model respond only to stimulus changes, there is no need for the subtractive comparison of motion in opposite directions, as is the case for most versions of the Reichardt model.

An important emergent property of the counterchange model is "recovery from biphasic inhibition," which occurs when the "Decrease" subunit is inhibited by an increase in input activation. Because of the time required for recovery from biphasic inhibition, the counterchange model does not require the explicit delay that is inherent in the Reichardt motion model in order to account for optimal motion perception sometimes occurring at non-zero ISIs.

Various versions of the Reichardt model failed to account for the results obtained for the generalized apparent motion perceived between two simultaneously visible surfaces. Although each of the subunits of the classical Reichardt detector responds in a sustained manner to changes in stimulation, the detector is presumably designed to respond to continuously moving stimuli that produce a succession of transient responses because moving stimuli would only briefly pass through each of the detector's subunits. That is, it is meant to correlate the transient presence of stimulation at each subunit location, not the continuously present stimulation that occurs for generalized apparent motion stimuli.

In contrast, the counterchange model accounts for results obtained for *both* generalized and standard two-flash apparent motion stimuli, all with the same set of parameter values. It thus provides a more parsimonious account than the Reichardt model for the perception of apparent motion between two element locations. The identical motion mechanism for both standard and generalized apparent motions is consistent with standard apparent motion being a special case of generalized apparent motion in which the lower luminance value of a stimulus is the same as the background luminance. More significantly, it shows that the perception of standard apparent motion (when a surface is

[4] The long and short path motions are not perceived simultaneously. If the counterchange model were extended to include inhibitory competition between motion detectors responding selectively to motion in opposite directions (Nichols, Hock, & Schöner, 2006), the perception of long path motion would have been signified most often for brief ISIs, and the perception of short path motion would have been signified most often for longer ISIs.

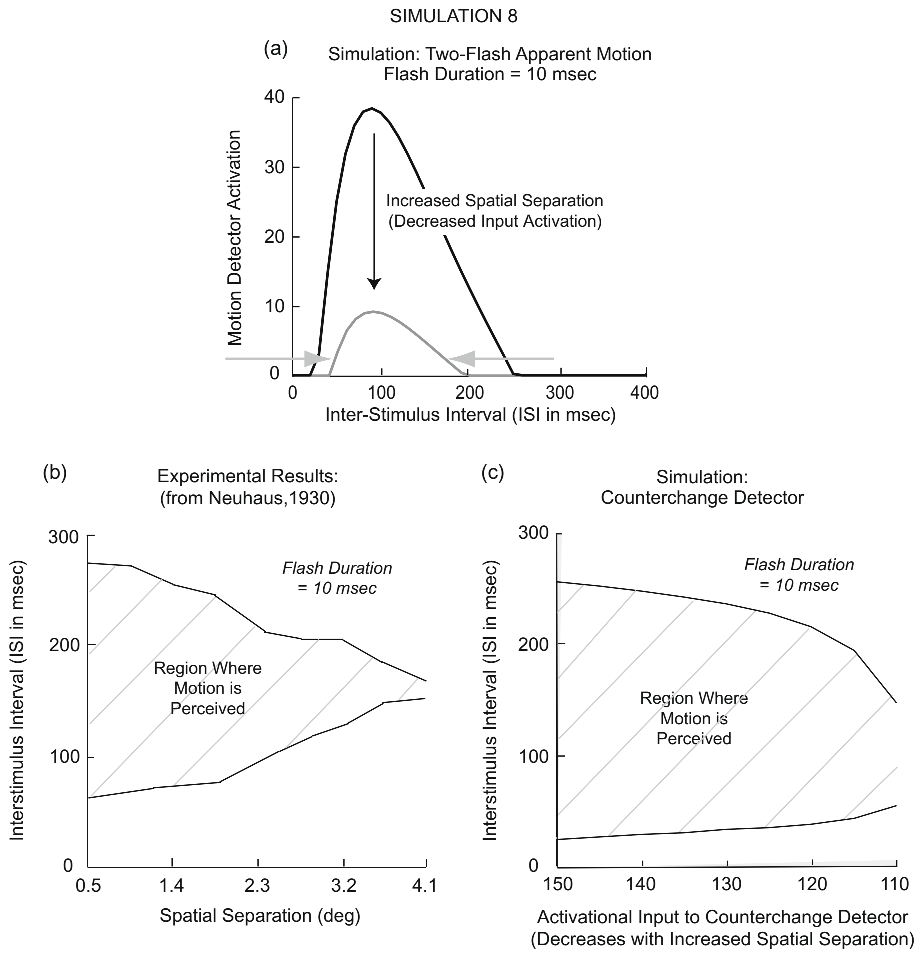

Fig. 11. Simulation 8. (a) The effects of inter-stimulus interval (ISI) and spatial separation on motion detector activation based on the counterchange model. It is assumed that changes in input activation become smaller with increases in spatial separation. (b) A subset of Neuhaus' (1930) results, re-formatted by Kolers (1972), showing effects of spatial separation on the ISI required in order for motion to be perceived, as per Korte's 3rd Law. (c) Simulation of Neuhaus' results based on the counterchange model.

displaced to a new location) can be accounted for by the detection of a pattern of counterchanging luminance contrast at the surface's previous and new location, rather than the detection of the location change itself.

9. Directional selectivity

In the various versions of the Reichardt detector, directional selectivity is established by temporally delaying the response of the subunit that would be excited first by motion in the detector's preferred direction. Conversely, Barlow and Levick's (1965) motion detector places the delay on the subunit that is excited first by motion in the detector's *null* direction. Directional selectivity is established by this subunit inhibiting the activation of the subunit that would be excited second by motion in the detector's null direction.

Torre and Poggio (1981) implemented this model with shunting inhibition (excitatory and inhibitory effects are combined on the dendrites of the motion detector), and more recently, Mo and Koch (2003) extended the model to also account for reverse-phi motion. The latter model includes pairs of ON-Center spatial filters that signal motion when there is no change in the luminance polarity of the displaced surfaces, and ON-Center/OFF-Center pairs that signal reverse-phi motion when luminance polarity changes. However, like the Reichardt model implemented in this article, the temporal filters of the model respond in a sustained, low-pass manner to changes in luminance. Thus, the model is as limited as the Reichardt model in its ability to account for whether or not motion is perceived between pairs of surfaces that are always visible; e.g., it would incorrectly signal motion when there is a sequence of luminance increases at two simultaneously visible spatial locations.

9.1. Simulation 10: directional selectivity by biphasic inhibition

The directional preference of counterchange detectors is determined by the relative location of the "Decrease" and "Increase" subunits. For example, when there is a flash at one location, then another flash to its right, a counterchange detector preferring rightward motion is activated (Fig. 13a). Motion is perceived because the excitatory state of the initially stimulated "Decrease" subunit overlaps in time with the subsequently stimulated "Increase" subunit. Motion is not perceived for a sequence of flashes in the reverse (null) direction because the excitatory state of the initially stimulated "Increase" subunit is followed by an inhibitory state resulting from the flash's offset, and the excitatory state of the subsequently stimulated "Decrease" subunit is preceded by the inhibitory state resulting from the second flash's onset (Fig. 13b). The effect is to temporally isolate the two excitatory phases, eliminating the possibility of a motion signal in the detector's null direction. Inhibitory interaction between subunits, as specified in Barlow and Levick's (1965) model and its subsequent versions, is not necessary when the subunits are biphasic.

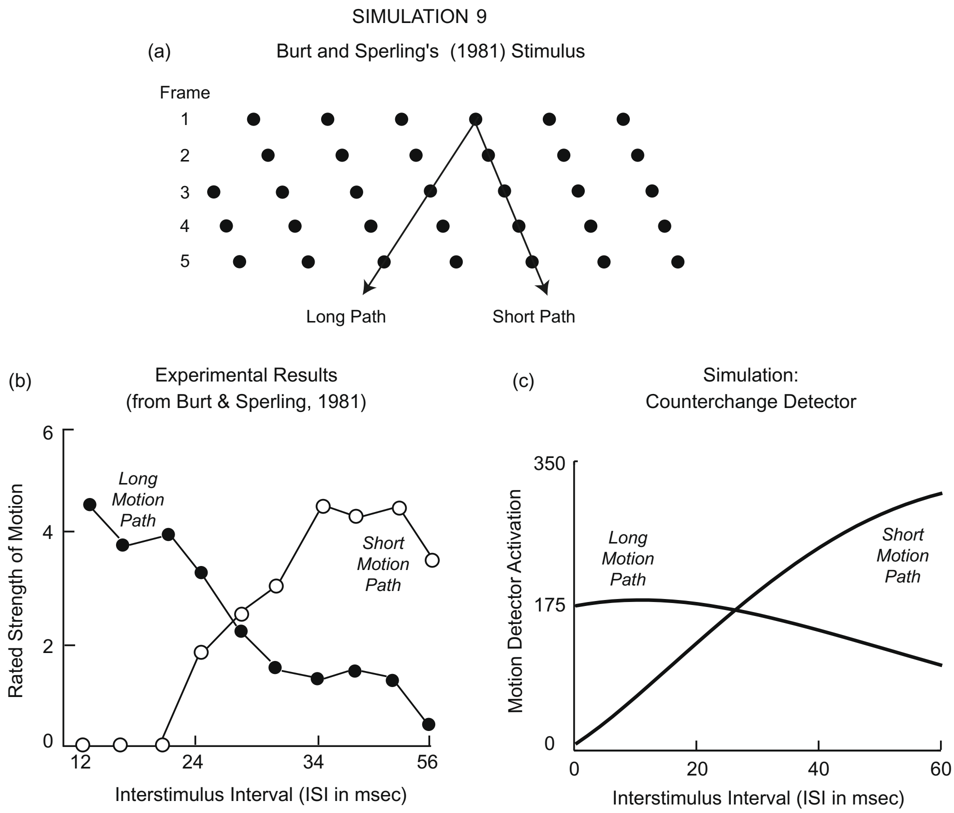

Fig. 12. Simulation 9. (a, b) Illustration of apparent motion stimulus and experimental results from Burt and Sperling (1981). (c) Simulation of experimental results based on the counterchange model. It is assumed that changes in input activation become smaller with increases in spatial separation.

10. Other motion phenomena

An important question is whether the counterchange principle is relevant to other forms of motion perception besides single-element apparent motion. To address this possibility it was assumed that the spatial input to the "Decrease" and "Increase" subunits of the counterchange motion detector is provided either by pairs of center/surround filters, pairs of edge filters (elongated receptive fields with one excitatory and one inhibitory lobe), or a combination of the two. It also was assumed that the filter pairs vary with respect to the spacing between them, with many filter pairs potentially activated by the same stimulus.

10.1. Drifting gratings

Although the drifting sine grating is the quintessential stimulus for Fourier-based motion energy models, it is possible for its motion to be perceived through the detection of counterchange (Fig. 14). To demonstrate this, it is assumed for this stimulus that the optimal input to the biphasic subunits of the counterchange detector comes from edge filters. As illustrated in Fig. 14, edge filters are maximally activated by sine gratings when they are stimulated by the luminance gradient lying between the peaks and troughs of the grating, provided that the filter's polarity is consistent with the luminance gradient (i.e., its excitatory lobe is stimulated by the lighter side of the luminance gradient). Edge filters are not activated when the luminance gradient is inconsistent with their polarity, and when they are stimulated by the luminance peaks or troughs of the sine grating. As the grating moves within the rectangular frame depicted in Fig. 14, activation is reduced for edge detectors that had just been maximally activated, and is increased for edge detectors that had just been minimally activated. This occurs optimally for pairs of filters that are 90 deg out of phase with respect to the spatial frequency of the drifting grating (Nakayama & Silverman, 1985), as illustrated in Fig. 14 for pairs of edge filters that differ in polarity.

To be sure, many other spatial filters would be activated at other locations that are not optimally spaced for the sine grating. Some would provide same-signed input that would not activate counterchange detectors, and others would provide oppositely signed input to counterchange detectors that would signal motion in the direction opposite to the displacement (Morgan & Cleary, 1992). However, counterchange-specified motion would be most strongly signaled by the filter pairs that happen to be 90 deg out of phase for the particular grating stimulating the filters. Detector activation in the direction of the displacement would be boosted by excitatory interactions with other pairs of filters that provide oppositely signed input to counterchange detectors for that direction, and could also be boosted by the priming of successive motions in the direction of the displacement (Hock & Balz, 1994; Snowden & Braddick, 1989). In addition, activation-dependent inhibitory interactions between counterchange detectors with dissimilar directional selectivity would suppress less strongly activated motion directions, resulting in the predominance of motion in the direction of the displacement (i.e., more strongly activated motion detectors would inhibit less strongly activated detectors more than vice versa; Nichols et al., 2006).

10.2. Short range motion for random-dot cinematograms

When a section of a random-dot cinematogram (RDC) composed of white and black elements is coherently displaced over a relatively small distance, so-called short range motion is perceived in the direction of the displacement (Bell & Lappin, 1973; Braddick, 1974; Lappin & Bell, 1976). Although this motion is usually attributed to the detection of motion energy (e.g., Cavanagh & Mather,

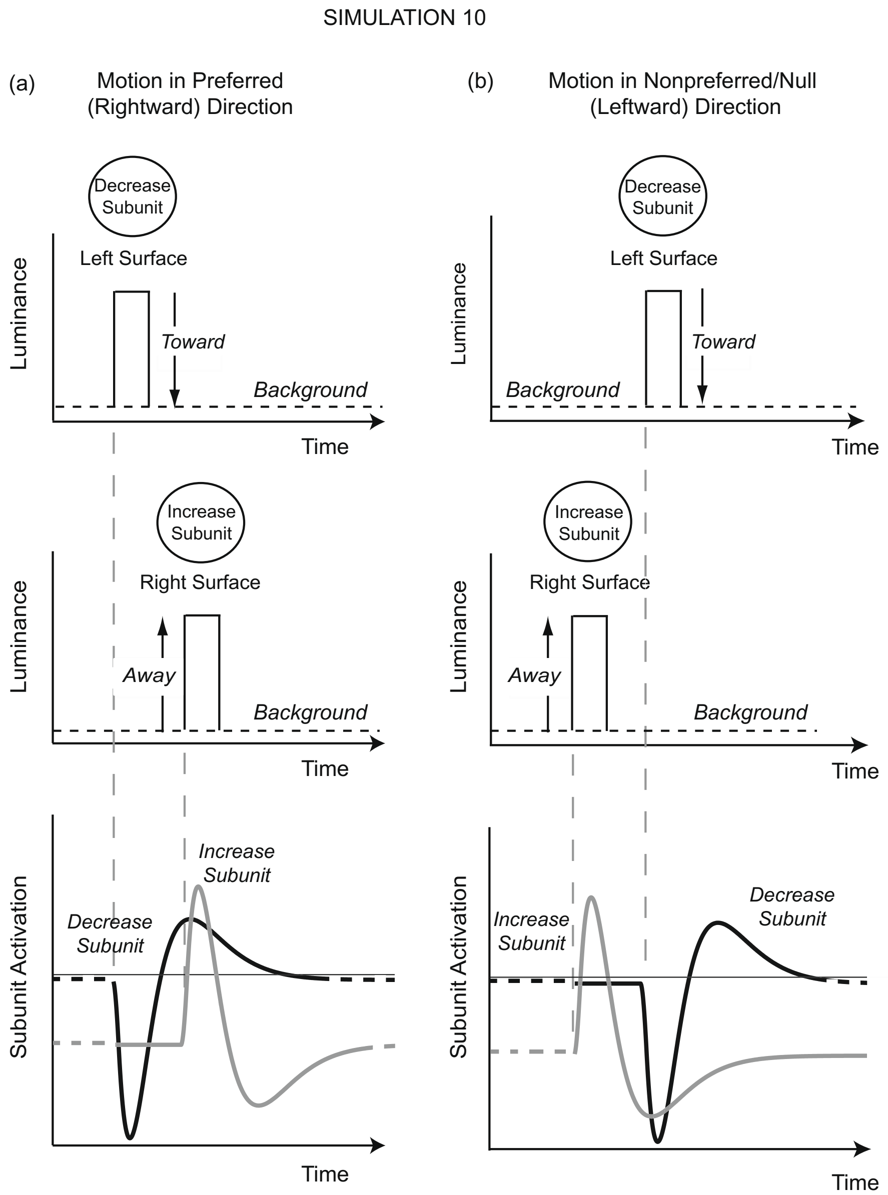

Fig. 13. Simulation 10. Illustration of how directional selectivity for two-flash stimuli results from biphasic inhibition in the counterchange model.

1989), it also is possible for it to be based on the detection of counterchange. This would require that the input to the biphasic subunits of the counterchange detector comes from spatial filters that have balanced excitatory and inhibitory regions that are large enough to be stimulated by multiple elements of the RDC. It is assumed for this analysis that the spatial filters have a center/surround organization, and further, that the entire RDC is "paved" by overlapping center/surround filters with excitatory centers and inhibitory surrounds, and an equal number of overlapping center/surround filters with inhibitory centers and excitatory surrounds.

The essential idea is that the difference in the number of white elements falling in the center vs. the surround zone of each filter will vary according to a binomial distribution with a mean of zero (approximated by a Gaussian distribution in Fig. 15). That is, when the RDC is first presented, clusters of elements in its to-be-displaced section will activate ON-center filters when there are more white elements in their center than their surround. Other element clusters will activate OFF-center filters with inhibitory centers when there are more white elements in their surround than their center.

An ON-Center filter with a center/surround white-difference that is greater than zero is indicated by the solid vertical line in Fig. 15. When the cluster of elements stimulating this filter is displaced, it will be replaced by another, randomly determined cluster of elements that on average will have a smaller center/surround white-difference (note the gray region under the Gaussian distribution in Fig. 15). As a result, the ON-center filter at that location will most often *decrease* in activation. In addition, when this cluster of elements is shifted to its new location, it will on average replace another, randomly determined cluster of elements for which there was a smaller center/surround white-difference, so most often the center/surround filter at that location will *increase* in activation. The input of this counterchanging activation to the biphasic subunits of the counterchange detector would result in motion being signaled in the direction of the displacement. (The same logic would apply to OFF-center filters.)

As is the case for drifting sine gratings, motion also will be signaled in directions other than the direction of displacement. Here again, excitatory interactions among motion detectors with similar directional selectivity would boost activation for all the motion

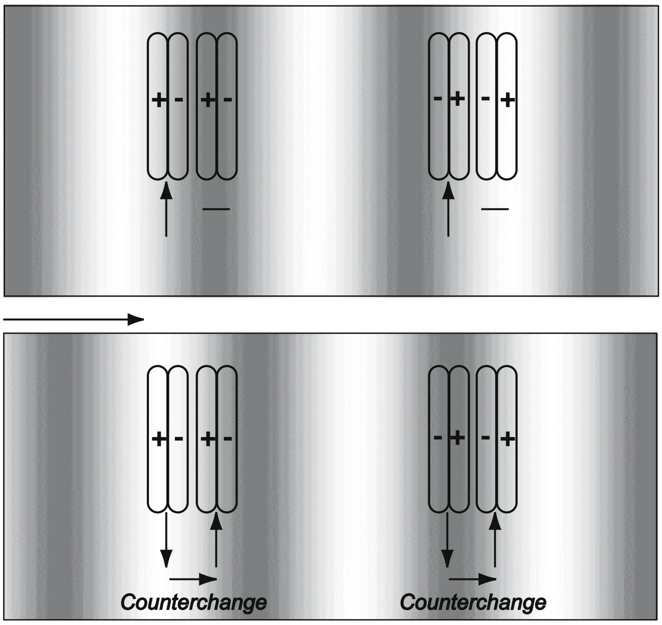

Fig. 14. Illustration of how the perception of motion for a drifting sine grating can be based on the detection of counterchange when the inputs to the biphasic subunits of the counterchange motion detector come from spatial filters with one excitatory and one inhibitory lobe (i.e., edge detectors). The optimal input for counterchange detection comes from pairs of filters that are 90° out of phase with respect to the spatial frequency of the sine grating.

detectors signaling motion in the direction in which the section of the RDC is coherently displaced, and inhibitory interactions among motion detectors with different directional selectivity will suppress motions that are not in that direction. A dynamical model incorporating these detector interactions was developed for RDCs by Williams, Phillips, and Sekuler (1986). The model demonstrates the power of cooperative excitatory/inhibitory interactions in creating a coherent motion direction for RDCs when motion is signaled in that direction by a very small percentage of its elements (Chang & Julesz, 1984; Williams & Sekuler, 1984).

10.3. The line motion illusion and continuous object motion

The line motion illusion occurs when one of two adjacent surfaces changes in luminance; it appears as if a new surface is moving in front of the initially presented surface. Hock and Nichols (in press) found that this motion is specified by counterchange; i.e., by oppositely signed changes in edge contrast and surface/background contrast. A schematic of the model shows that the arrangement of edge and center/surround filters which suffices for the perception of the line motion illusion (Fig. 16a) could also account for the perception of continuous object motion (Fig. 16b).

11. Other motion models

There is no shortage of motion detection models in the literature. Two are selected here for further discussion. The first, by Grossberg and Rudd (1992), addresses a wide range of apparent motion phenomena, including some that are simulated in the current article. The second, Lu and Sperling's (1995) three-systems model, provides a context for the relationship between counterchange and Reichardt/motion energy detection.

11.1. Grossberg and Rudd (1992)

Motion detection in Grossberg and Rudd's (1992) model is local to the individual surfaces undergoing luminance change. Sustained responses to the luminance contrast at the edges of a surface are multiplicatively combined with transient responses to its changing luminance, signaling expanding and contracting gamma motion for the surface. Apparent motion *between* a pair of surface locations requires that each local motion detector's activation spread to surrounding regions – a Gaussian-shaped spatial distribution of activation is assumed - and for the distributions for the two surfaces to be close enough for their sum to form a single-peaked Gaussian. The peak of the summed-Gaussian shifts over time as motion detector activation goes down at one location and up at the other. This shift constitutes their *G-wave*.

Grossberg and Rudd's (1992) model does not compute a motion signal to characterize whether or not apparent motion will be detected between a pair of locations. A case in point occurs for the stimulus illustrated in Fig. 6b. For this stimulus, the luminance/contrast at one location is greater than that of the other during the first frame, then luminance/contrast increases unequally at the two locations during the second frame such that it becomes greater at the second location. With respect to Grossberg and Rudd's (1992) model, there would be much more motion detector activation for the surface with the larger increase in luminance/contrast. This would result in more motion detector activation for that surface, and the resulting spread of activation for the two changing surfaces would shift the peak of the summed-Gaussian toward the location with the greater change in luminance/

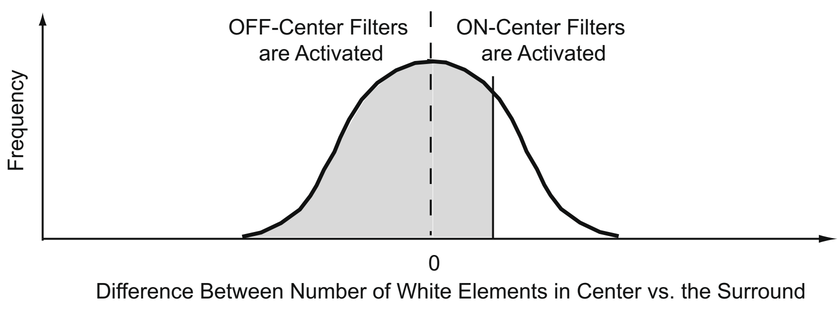

Fig. 15. When center/surround spatial filters "cover" a random-dot cinematogram (RDC) composed of white and black elements, the activation of each filter depends on whether there are more white dots falling in its excitatory vs. its inhibitory zone. The center/surround difference in white elements varies over the ON- and OFF-Center filters covering the RDC according to a binomial distribution (approximated by a Gaussian distribution) with a mean difference of zero. The gray region in the distribution indicates that when an ON-Center filter is activated by a cluster of white and black elements (the center/surround white-difference is positive), it is likely that the filter's activation will go down when the cluster of elements is shifted to another location; i.e., the shifted elements are more likely to be replaced by elements with a smaller rather than a larger white-difference. The gray region also indicates that activation is likely to increase for ON-Center filter at the location where the elements will be re-located; they will replace elements that are more likely to have had a smaller rather than a larger center/surround white-difference. The decrease in activation at one location and the increase in activation at the new location makes it plausible that counterchange detection is responsible for the perception of short range motion.

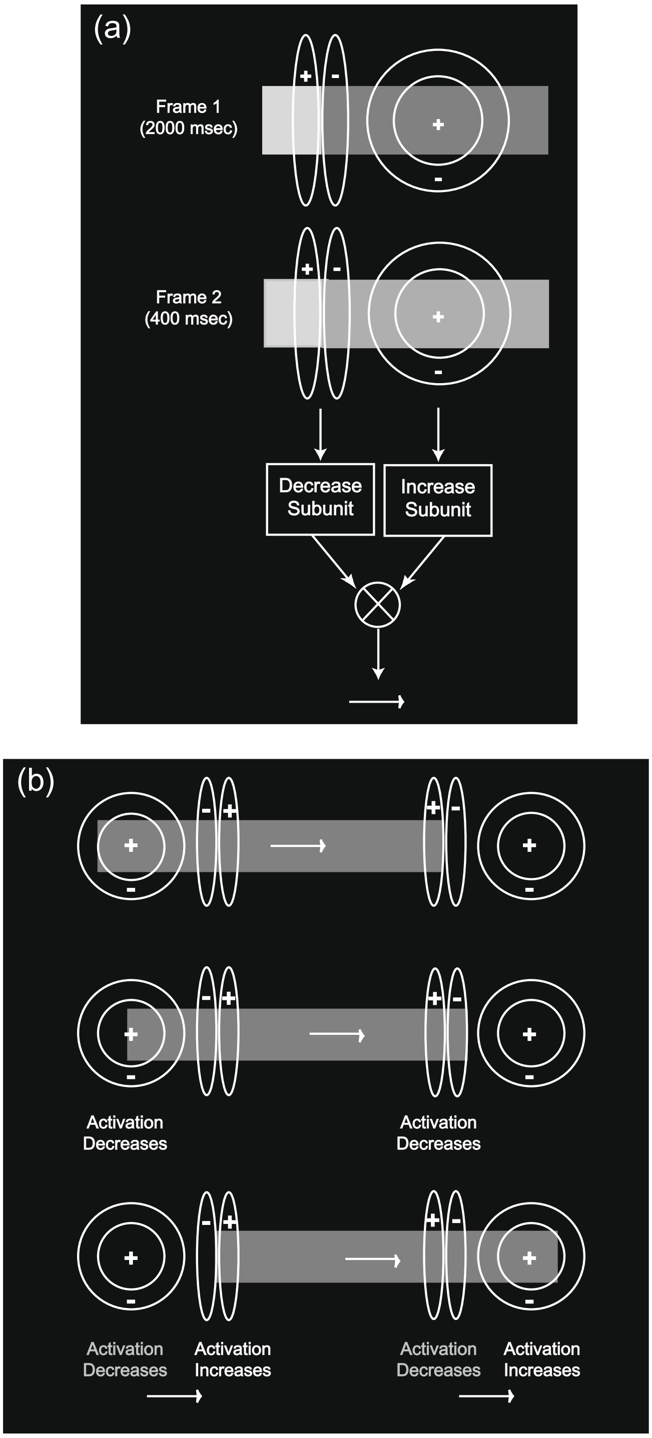

Fig. 16. (a) Counterchange model for a generalized version of the line motion illusion. Perceived motion is rightward for this example. It appears as if the lighter surface is sliding across the darker surface. (b) Counterchange model with spatial inputs from edge and center/surround filters as applied to the perception of continuous object motion.

contrast. Nonetheless, motion is not perceived (Hock et al., 2002). It might be argued that this is because the shifts in the peak are too small to be detected. Perhaps so. The problem is that there is no detection mechanism in the Grossberg and Rudd (1992) model to determine whether or not this shifts in the peak of the summed-Gaussian are above or below threshold.

In contrast, the counterchange motion mechanism directly detects apparent motion *between* pairs of surface locations rather than deriving motion indirectly from motion signals associated with individual surfaces. "Recovery from biphasic inhibition" and the limited duration of the biphasic subunits' transient responses provide a relatively simple basis for the counterchange model's simulation of Kolers' (1964) inverted-U function relating frame duration and ISI (Fig. 10b), Sgro's (1963) experimental study of Korte's 4th law (Fig. 10c), Neuhaus' (1930) experimental study of Korte's 3rd law (Fig. 11), and Burt and Sperling's (1981) results entailing motion perceived over long vs. short paths (Fig. 12). Perhaps because they base transient detection on time derivatives rather than biphasic detection, Grossberg and Rudd's (1992) more complex account of these phenomena entails shunting membrane equations, habituation of transmitter gates, long-range Gaussian filters, and slow changing spatial input (the latter from Francis & Grossberg, 1996).

11.2. *Lu and Sperling (1995)*

In Lu and Sperling's (1995) three-systems theory, 1st-order motion entails changes in the spatial distribution of luminance and 2nd-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. Their 3rd-order system is based on attentionally modulated changes in salience/activation which are created by stimulus attributes changing at different spatial locations.

Hock and Nichols (2004) have shown that counterchange detection is a viable mechanism for 3rd-order motion perception. The stimuli in their experiments were composed of six adjacent rectangles with successively greater luminance values. Sequential increments in luminance contrast, starting with the darkest rectangle, created 1st- and 2nd-order motion energy in the direction of the luminance changes. Counterchanging edge and surface-to-background contrast specified motion in the opposite direction, so if motion were perceived in the counterchange-specified direction, it could not have been due to either 1st- or 2nd-order motion.

The perceived motion direction for this stimulus depended on frame duration. For brief durations (fast speeds), motion was more likely in the motion energy than in the counterchange-specified direction. It had an "objectless" quality that Sperling and Lu (1998) ascribe to 1st- and 2nd-order motion energy. For longer frame durations, motion was perceived in the counterchange-specified direction; a succession of surfaces appeared to be sliding in front of the surface adjacent to it, giving the counterchange-specified motion the quality of object motion that Sperling and Lu (1998) ascribe to 3rd-order motion. Hock and Nichols (2004) results suggest, therefore, that there are dual pathways for motion perception. One is based on Reichardt/motion energy detectors with relatively fast temporal parameters that respond to the motion energy in the stimulus, and the other on the counterchange detectors studied in this article.

12. Conclusion

The phenomenological impression of sequence for continuously moving objects has had a very strong influence on the development of theories of motion perception. Sensitivity to sequence is explicit for Reichardt-style models, which delay the response of one of its subunits in order to bring it into temporal alignment with the response of its other subunit. It is implicit in motion energy theories, for which motion is at least approximately specified by the centroid of a stimulus' luminance profile shifting through a sequence of spatial locations. Experimental results (Gilroy & Hock, in press), together with the computational results reported in the current article, provide evidence for a non-sequential, counterchange basis for the perception of motion. The non-sequential stimulus information entails spatial patterns encompassing changes in contrast for the boundaries and surfaces of objects, stimulus information that is also essential for the perception of object shape. One goal, which is shared with the "formotion" model (Francis & Grossberg, 1996; Baloch & Grossberg, 1997), is to provide a common informational basis for the perception of object motion and object shape. This would minimize the binding problem that would arise were the perception of an object's motion based on different stimulus information (e.g., motion energy) than the perception of its shape. The second goal is to show that the counterchange mechanism applies to motion resulting from changes in any object attribute. This mechanism, which we think is the basis for Lu and Sperling's (1995) 3rd-order motion, would entail the detection of decreases in activation due to attribute changes at one location, and simultaneous or sequential increases in activation due to attribute changes at a second location.

Appendix

Counterchange motion detector

Visual stimuli are represented in the model by time-varying input functions $S(x,t)$ at the two locations, x = right and x = left, where t stands for time. For each experiment, these time functions model the luminance profiles illustrated in Figs. 3–13. The associated parameter values for the size and duration of the step-wise stimulus changes are listed below.

The biphasic transient detectors for subunits' response to decreases (dec) and increases (inc) in input activation, illustrated in Fig. 2, depend on time differences, Δt as proposed by Adelson & Bergen (1985, this is the case $n = 1$ of their Eq. (1)):

$$T_{\rm dec}(\Delta t) = -\frac{\Delta t}{\tau_{\rm tr}} \exp\left[-\frac{\Delta t}{\tau_{\rm tr}}\right]\left(1 - \frac{(\Delta t)^2}{6\tau_{\rm tr}^2}\right) \quad (1)$$

$$T_{\rm inc}(\Delta t) = -\frac{\Delta t}{\tau_{\rm tr}} \exp\left[-\frac{\Delta t}{\tau_{\rm tr}}\right]\left(1 - \frac{(\Delta t)^2}{6\tau_{\rm tr}^2}\right) \quad (2)$$

where $\tau_{\rm tr}$ = 30 ms determines the time scale of the response.

Half-wave rectification is applied to any activation level, u:

$$\Theta(u) = \begin{cases} u & \text{for } u \geqslant 0 \\ 0 & \text{for } u < 0 \end{cases} \quad (3)$$

Therefore, the half-wave rectified transient representation of a stimulus $S(x,t)$ at location, x (x = right or x = left) and time t is:

$$S_{\rm dec}(x,t) = \Theta\left(\int_{-\infty}^{t} dt' \quad T_{\rm dec}(t-t')S(x,t')\right) \quad (4)$$

$$S_{\rm inc}(x,t) = \Theta\left(\int_{-\infty}^{t} dt' \quad T_{\rm inc}(t-t')S(x,t')\right) \quad (5)$$

The dynamic neurons, $u_{\rm tr,dec}(x,t)$ and $u_{\rm tr,inc}(x,t)$, represent transient responses of sub-units that respond with excitation to decreases and increases in stimulus level, respectively. Their dynamics at location, x = right or left, and time, t, is:

$$\tau\dot{u}_{\rm tr,dec}(x,t) = -u_{\rm tr,dec}(x,t) + h_{\rm tr,dec} + S_{\rm dec}(x,t) \quad (6)$$

$$\tau\dot{u}_{\rm tr,inc}(x,t) = -u_{\rm tr,inc}(x,t) + h_{\rm tr,inc} + S_{\rm inc}(x,t) \quad (7)$$

where $h_{\rm tr,dec} = -10$ is the resting level of the "Decrease" subunits and $h_{\rm tr,inc} = -300$ is the resting level of the "Increase" subunits.

The half-wave rectified activation level of these neurons are combined into motion detector signals, S(right, t) and S(left, t):

$$S(\text{right},t) = [\Theta(u_{\rm tr,dec}(left,t))\Theta(_{\rm tr,inc}(right,t))]^{1/2} \quad (8)$$

$$S(left,t) = [\Theta(u_{\rm tr,dec}(right,t))\Theta(_{\rm tr,inc}(left,t))]^{1/2} \quad (9)$$

which are inputs into dynamic neurons, $u(i,t)$, representing motion detection for each motion direction, i = rightward or i = leftward:

$$\tau\dot{u}(i,t) = -u(i,t) + h + S(i,t) \quad (10)$$

where τ = 10 ms is the time scale and $h = -20$ is the resting level. The coupling of these dynamic neurons is neglected here, but forms the basis for understanding the formation of motion patterns (Hock, Schöner, & Giese, 2003).

Reichardt motion detector

The Reichardt model uses monophasic low-pass filters

$$T_{\rm Reich}(\Delta t) = \left(\frac{\Delta t}{\tau_{\rm tr}}\right)^n \frac{1}{2}\frac{1}{n!} \exp\left[-\frac{\Delta t}{\tau_{\rm tr}}\right] \quad (11)$$

with the same time constant, $T_{\rm tr}$ = 30 ms, as the counterchange model as well as the same order ($n = 1$). The resultant half-wave rectified sustained stimulus representation for each location, x, is:

$$S_{\rm Reich}(x,t) = \Theta\left(\int_{-\infty}^{t} dt' \quad T_{\rm Reich}(t-t')S(x,t')\right). \quad (12)$$

From these, the motion signal for rightward and leftward motion is computed by multiplying the response at the initial location, delayed by $\Delta\tau$ = 100 ms, with the response at the target location:

$$M_{\rm Reich}(\text{rightward},t) = [\Theta(S_{\rm Reich}(\text{left},t-\Delta\tau))\Theta(S_{\rm Reich}(\text{right},t))]^{1/2} \quad (13)$$

$$M_{\rm Reich}(\text{leftward},t) = [\Theta(S_{\rm Reich}(\text{right},t-\Delta\tau))\Theta(S_{\rm Reich}(\text{left},t))]^{1/2} \quad (14)$$

Finally, the two opposing motion signals are subtracted from each other and motion is indicated if the difference is larger than a threshold (chosen as 20, as in the counterchange model):

$$D_{\rm Reich}(\text{rightward},t) = \Theta[M_{\rm Reich}(\text{rightward},t) - M_{\rm Reich}(\text{leftward},t) - 20] \quad (15)$$

$$D_{\rm Reich}(\text{leftward},t) = \Theta[M_{\rm Reich}(\text{leftward},t) - M_{\rm Reich}(\text{rightward},t) - 20] \quad (16)$$

Simulations

Each set of simulations of the different experiments used the same values for all model parameters and differed only through the stimulus. The input activation time functions, $S(x,t)$, at the two locations, x = right and x = left are listed here individually for each set of simulations. The same input levels are applied for both the counterchange and Reichardt models. The stimuli in each simulation are parameterized as follows (all times are in ms).

Simulation 1. For the stimuli illustrated in Fig. 3a and b:

When the *Toward* change precedes the *Away* change

S(left, t) = 120 for $0 < t \leqslant 2000$
S(left, t) = 40 for $2000 < t \leqslant 4000$
S(left, t) = 0 for $4000 < t$
S(right, t) = 120 for $0 < t \leqslant 2000$ + ICI

S(right, t) = 200 for $2000 + \text{ICI} < t \leqslant 4000$
S(right, t) = 0 for $4000 < t$

When the *Away* change precedes the *Toward* change

$S(\text{left}, t) = 120$ for $0 < t \leqslant 2000 + \text{ICI}$
$S(\text{left}, t) = 40$ for $2000 + \text{ICI} < t \leqslant 4000$
$S(\text{left}, t) = 0$ for $4000 < t$
$S(\text{right}, t) = 120$ for $0 < t \leqslant 2000$

$S(\text{right}, t) = 200$ for $2000 < t \leqslant 4000$
$S(\text{right}, t) = 0$ for $4000 < t$

ICI is the inter-change interval, which varies from 0 to 400 ms.

Simulation 2. For the stimulus illustrated in Fig. 5a:

$S(\text{left}, t) = 120$ for $0 < t \leqslant 2000$
$S(\text{left}, t) = 200$ for $2000 < t \leqslant 4000$
$S(\text{left}, t) = 0$ for $4000 < t$
$S(\text{right}, t) = 120$ for $0 < t \leqslant 2000 + \text{ICI}$

$S(\text{right}, t) = 200$ for $2000 + \text{ICI} < t \leqslant 4000$
$S(\text{right}, t) = 0$ for $4000 < t$

ICI is the inter-change interval, which varies from 0 to 400 ms.

Simulation 3. For the stimulus illustrated in Fig. 6a and b:

For the Counterchange condition

$S(\text{left}, t) = 162$ for $0 < t \leqslant 267$
$S(\text{left}, t) = 94$ for $268 < t \leqslant 534$
$S(\text{right}, t) = 94$ for $0 < t \leqslant 267$

$S(\text{right}, t) = 162$ for $268 < t \leqslant 534$
or
$S(\text{right}, t) = 100$ for $0 < t \leqslant 267$
$S(\text{right}, t) = 156$ for $268 < t \leqslant 534$
or
$S(\text{right}, t) = 106$ for $0 < t \leqslant 267$
$S(\text{right}, t) = 152$ for $268 < t \leqslant 534$
or
$S(\text{right}, t) = 112$ for $0 < t \leqslant 267$
$S(\text{right}, t) = 146$ for $268 < t \leqslant 534$

For the Co-change condition.

$S(\text{left}, t) = 94$ for $0 < t \leqslant 267$
$S(\text{left}, t) = 162$ for $268 < t \leqslant 534$
$S(\text{right}, t) = 26$ for $0 < t \leqslant 267$

$S(\text{right}, t) = 232$ for $268 < t \leqslant 534$
or
$S(\text{right}, t) = 30$ for $0 < t \leqslant 267$
$S(\text{right}, t) = 226$ for $268 < t \leqslant 534$
or
$S(\text{right}, t) = 36$ for $0 < t \leqslant 267$
$S(\text{right}, t) = 220$ for $268 < t \leqslant 534$
or
$S(\text{right}, t) = 42$ for $0 < t \leqslant 267$
$S(\text{right}, t) = 214$ for $268 < t \leqslant 534$

Simulation 4. For the stimulus illustrated in Fig. 7a.

$S(\text{left}, t) = 80$ for $0 < t \leqslant 2000$
$S(\text{left}, t) = 40$ for $2000 < t \leqslant 2400$
$S(\text{left}, t) = 0$ for $2400 < t$
$S(\text{right}, t) = 80$ for $0 < t \leqslant 2000$

$S(\text{right}, t) = 120$ for $2000 < t \leqslant 2000 + \text{DUR}$
$S(\text{right}, t) = 0$ for $2000 + \text{DUR} < t$

DUR is the time duration preceding the removal of the right element, for which there was previously an increase in luminance (it varied from 0 to 400 ms).

Simulation 5. For the stimulus illustrated in Fig. 8a:

$S(\text{left}, t) = 4$ for $0 < t \leqslant 2000$
$S(\text{left}, t) = 80$ for $2000 < t \leqslant 2000 + \text{DUR}$
$S(\text{left}, t) = 0$ for $2000 + \text{DUR} < t$
$S(\text{right}, t) = 80$ for $0 < t \leqslant 2000 + \text{DUR}$

$S(\text{right}, t) = 180$ for $2000 + \text{DUR} < t \leqslant 2400 + \text{DUR}$
$S(\text{right}, t) = 0$ for $2400 + \text{DUR} < t$

DUR is the time duration preceding the removal of the left element, for which there was previously an increase in luminance (it varied from 0 to 400 ms).

Simulation 6. For the stimulus illustrated in Fig. 9a:

$S(\text{left}, t) = 120$ for $0 < t \leqslant \text{FD}$
$S(\text{left}, t) = 0$ for $\text{FD} < t$
$S(\text{right}, t) = 0$ for $0 < t \leqslant \text{FD} + \text{ISI}$

$S(\text{right}, t) = 120$ for $\text{FD} + \text{ISI} < t \leqslant 2 \cdot \text{FD} + \text{ISI}$
$S(\text{right}, t) = 0$ for $2 \cdot \text{FD} + \text{ISI} < t$

FD is the frame/flash duration (300 or 20 ms), and ISI is the inter-stimulus interval (0 or 78 ms).

Simulation 7. Same as Simulation 6 except that: (1) the flash/frame duration (FD) is 20 ms and the inter-stimulus interval (ISI) varies between 0 and 600 ms (Fig. 10b), and (2) FD is varied and the ISI for which motion is optimally signified is determined (Fig. 10c).

Simulation 8. Same as Simulation 6 except that the frame/flash duration (FD) is 10 ms, the inter-stimulus interval (ISI) varies between 0 and 300 ms, and the magnitude of the flashes, which is 120 in Simulation 6, varies between 110 and 150 in units of 5 for the simulation in Fig. 11c (reflecting differences in spatial separation). The flash magnitudes are 115 and 140 for the simulation in Fig. 11a.

Simulation 9. Same as Simulation 6 except that the frame/flash duration (FD) is 20 ms, the inter-stimulus interval (ISI) varies between 0 and 60 ms, and the magnitude of the flash, which is 120 in Simulation 6, is 130 for the short motion path and 45 for the long motion path (Fig. 12c).

Simulation 10. Same as Simulation 6 except that the frame/flash duration (FD) is 200 ms, and the inter-stimulus interval (ISI) is 100 ms (Fig. 13).

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