



The independent detection of motion energy and counterchange: Flexibility in motion detection



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ABSTRACT

Motion perception is determined by changing patterns of neural activation initiated by spatiotemporal changes in stimulus features. Motion specified by 1st-order motion energy entails neural patterns that are initiated by spatiotemporal changes in luminance, whereas motion specified by counterchange entails oppositely signed changes in neural activation that can be initiated by spatiotemporal changes in any feature. A constraint in furthering this distinction is that motion energy and counterchange are co-specified by most visual stimuli. In the current study, counterchange was isolated for stimuli composed of translating subjective (Kanizsa) squares, surfaces created by the visual system. Motion energy was isolated for stimuli composed of sequences of luminance increments that spread across perceptually stationary, literal surfaces. Counterchange-specified motion was perceived over a wide range of frame durations, and preferentially for short motion paths. Motion specified by motion energy was diminished for relatively long frame durations, and was unaffected by the length of the motion path. Finally, it was found that blank inter-frame intervals can restore counterchange-specified motion perception for frame durations that are otherwise too brief for motion to be perceived. The results of these and earlier experiments suggest that 1st-order motion energy mechanisms, dedicated to the detection of changes in neural activation initiated by spatiotemporal changes in luminance, provide the basis for objectless motion perception (Wertheimer's phi motion). In contrast, counterchanging neural activation initiated by spatiotemporal changes in any feature, including features created by the visual system, provides a flexible basis for the perception of object motion (Wertheimer's beta motion).

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1. Introduction

It is commonplace to consider any neuron that responds to a visual stimulus as a detector of information present in the stimulus. In reality, however, this is shorthand for the fact that the optical effects of the stimulus feed forward through many layers in the visual system, starting with the retinal photoreceptors. Consequently, neurons at any location in the visual system are not responding directly to optical information falling on the retina, but are instead responding to patterns of neural activation that are initiated by the optical information and transformed as the neural representation of the stimulus passes forward to higher levels in the visual system. Simoncelli and Heeger (1998) refer to this as a “neural image” of the stimulus.

The objective of the research reported in this article is to compare two motion detecting mechanisms, one activated by spatiotemporal changes in luminance and the other by counterchange (i.e., the activational effect of a feature decreasing at one location and increasing at another). The comparison is with respect to their spatial and temporal dependence, and their flexibility with respect to different kinds of motion-specifying stimulus information. Also discussed is the possibility that these mechanisms are related to Lu and Sperling's (1995) 1st- and 3rd-order motion systems.

For one mechanism, which in its most recent form entails the detection of 1st-order motion energy (Adelson & Bergen, 1985; van Santen & Sperling, 1985), motion-specifying patterns of neural activation are specifically linked to spatiotemporal changes in luminance. For the other mechanism, which entails the detection of counterchange, a particular pattern of neural activation is required in order for motion to be perceived, namely a decrease in activation at one location and an increase in activation at another (Hock, Gilroy, & Harnett, 2002; Hock, Schöner, & Gilroy, 2009). However, unlike motion energy detection, counterchange

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detection is not tied to a particular kind of optical information, and as will be shown, can be influenced by neural processes that create patterns of neural activation rather than just feeding stimulus information forward from the retina.

1.1. Luminance-specified motion (1st-order motion energy)

The detection of luminance-specified motion is the basis for Reichardt's original model of motion detection (Hassenstein & Reichardt, 1956), which correlates the pattern of activation for luminance-stimulated photoreceptors at one moment in time with the same pattern, shifted in location, at a second moment in time. Pairs of subunits receive the photoreceptor activity produced by the stimulus as their input, with directionally selective motion computed by delaying the response of one subunit of the pair and then multiplying it by the response of the second, undelayed subunit. In Barlow and Levick's (1965) model, motion detection is based on the pattern of activation of retinal bipolar cells, again resulting from spatiotemporal changes in luminance. Pairs of subunits receive bipolar cell activity produced by the stimulus as their input, with directionally selective motion computed by multiplying the outputs of the two subunits, one of which inhibits the excitation of the other.

Subsequent models, which entail the detection of 1st-order motion energy (Adelson & Bergen, 1985; van Santen & Sperling, 1985), base their computations on activation at the retinal ganglion cell level, or higher, of receptive fields (spatial filters) with balanced excitatory and inhibitory zones. Again, the pattern of spatial filter activation is determined by spatiotemporal changes in luminance. Motion energy computations based on these neural activation patterns have the distinctive feature that they are Fourier based, which requires a quadrature relationship between pairs of spatial filters whose activation provides the input for the computation of 1st-order motion energy. That is, pairs of filters that are further apart must be larger compared with pairs of filters that are closer together such that both filters of a pair are most strongly activated by sine gratings of a particular spatial frequency with phases separated by 90 deg relative to the other. This quadrature relationship is necessary in order for each filter pair to be approximately band-pass in the Fourier domain.

The Fourier basis of motion energy models makes displaced sine gratings optimal and therefore much studied stimuli for motion energy detection. However, Hock, Schöner, and Gilroy (2009) have shown that the motion of sine gratings also can be accounted for by the detection of counterchange; e.g., decreased contrast where the grating's peak is displaced onto the center of a balanced filter, accompanied by increased contrast where the maximally sloped portion of the grating is displaced onto a paired balanced filter. In order to avoid this confound, a stimulus was designed that eliminates the detection of counterchange and thereby isolates the contribution of spatiotemporal changes in luminance to the perception of motion.

The stimulus is composed of four simultaneously visible, horizontally aligned square surfaces whose luminance is sequentially incremented, either from left-to-right (as in Fig. 1) or from right-to-left. Although motion is perceived, none of the square surfaces appear to move. Instead, continuous spreading-luminance motion is perceived across the four perceptually stationary squares (Movie 1; the viewer should attend to the central fixation dot for this and the other supplementary movies included in this article). The motion percept depends only on spatiotemporal changes in luminance; there are no luminance decrements (or decreases in contrast) to accompany the luminance increments (or increases in luminance contrast), so no counterchange is present. It is called a *ME (motion energy)* stimulus, consistent with the understanding of 1st-order motion energy as entailing spatiotemporal changes in "raw" lumi-

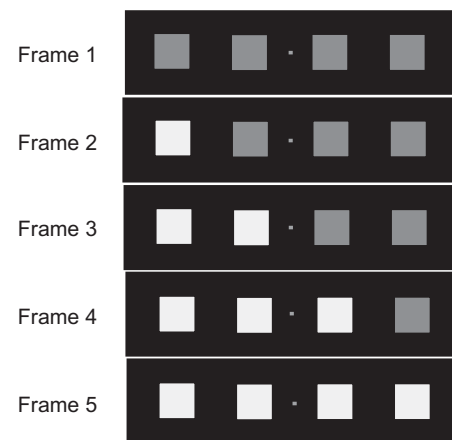


Fig. 1. An *ME (motion energy)* stimulus for which there is rightward motion energy, but no counterchange-specified motion. It was tested in Experiment 1.

nance (Chubb & Sperling, 1988) or spatiotemporal changes in the luminance profile of a stimulus (Cavanagh & Mather, 1989), without appeal to a particular model for the computation of motion energy.¹

1.2. Counterchange-specified motion

The counterchange motion detector is composed of two change-detecting subunits, one excited by decreases in its input activation and the other by increases in its input activation. Directionally selective motion is computed by the multiplication of the subunits' outputs, with motion beginning at the location of decreased activation and ending at the location of increased activation. Hock, Gilroy, and Harnett (2002) showed this for surfaces with uniform luminance: motion began at the surface whose luminance contrast with its background decreased and ended at a nonadjacent surface whose luminance contrast with its background increased. Counterchange-specified motion also can be perceived when the luminance contrast at the boundary of two adjacent surfaces is changed by changing the luminance of one of the surfaces (Hock & Nichols, 2010, 2013). This motion percept, which is related to the line motion illusion (Hikosaka, Miyauchi, & Shimojo, 1993a, 1993b), indicates that the counterchange computation can occur at a neural level where activational input comes from edge detectors (Area V1). Oppositely signed changes in the background-relative texture contrast of two nonadjacent checkerboard surfaces with their checkerboard background also can result in the perception of motion (Gilroy & Hock, 2004), indicating that counterchange can be computed from changes in extra-striate levels of neural activation (Smith et al., 1998). Finally, counterchange-specified motion can be perceived when at one location there is a change in the luminance contrast of a uniform surface with its uniform background, and at another non-adjacent location there is an oppositely signed change in the texture contrast of a checkerboard surface with its checkerboard background (Hock & Gilroy, 2005). This result was important because it showed that the counterchange principle entails a particular pattern of activation change, but is

¹ The applicability of Fourier-based models for computing the motion energy of spatially and temporally discontinuous multi-frame stimuli, like those in the current study, is problematic. It was found for these stimuli that Adelson and Bergen's (1985) motion energy detector is excessively sensitive to small differences in filter size and small differences in the extent to which the background is incorporated into the computation. Such small changes often result in the reversal of the computed direction of the motion energy and the incorrect prediction of motion perception outside the spatial span of the stimulus.

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