How do representations of visual form organize our percepts of visual motion?

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Abstract

How does the visual system generate percepts of moving forms? How does this happen when the forms are emergent percepts (such as illusory contours or segregated textures) and the motion percept is apparent motion between the emergent forms? A neural model of form-motion interactions is developed to explain parametric properties of psychophysical motion data and to make predictions about the parallel cortical processing streams V1 → MT and V1 → V2 → MT. The model simulates many parametric psychophysical data arising from form-motion interactions. A key linkage between form and motion data is articulated in terms of properties of visual persistence and properties of apparent motion. The model explains how an illusory contour can move in apparent motion to another illusory contour or to a luminance-derived contour; how illusory contour persistence relates to the upper ISI threshold for apparent motion; and how upper and lower ISI thresholds for seeing apparent motion between two flashes decrease with stimulus duration and narrow with spatial separation (Korte's laws). Psychophysical data are derived from an analysis of how orientationally tuned form perception mechanisms and directionally tuned motion perception mechanisms interact to generate consistent percepts of moving forms.

Introduction

This article explains how the dynamic properties of a neural network theory of visual form processing proposed by Grossberg & Mingolla (1985a,b, 1987) and analyzed dynamically in Grossberg (1991) and Francis, Grossberg & Mingolla (1993, 1994) contributes to properties of perceived motion. The theory suggests that many temporal aspects of apparent motion depend on the time taken to reset a visual segmentation generated by form-processing mechanisms. Psychophysical studies of apparent motion of moving forms reveal three key sets of data, which are all explainable by the model.

- Illusory contours can move in apparent motion and do not obey the inverse relationship between upper interstimulus interval (ISI) thresholds and stimulus duration characteristic of luminance-based contours (Mather, 1988; Ramachandran, 1985; von Grünau, 1979).

- Apparent motion can occur between one stimulus defined by illusory contours and a second stimulus defined by luminance contrast (Cavanagh, Arguin & von Grünau, 1989; von Grünau, 1979).

- For luminance-based stimuli both upper and lower ISI thresholds are inversely related to flash duration. The range of ISIs capable of producing apparent motion nar-
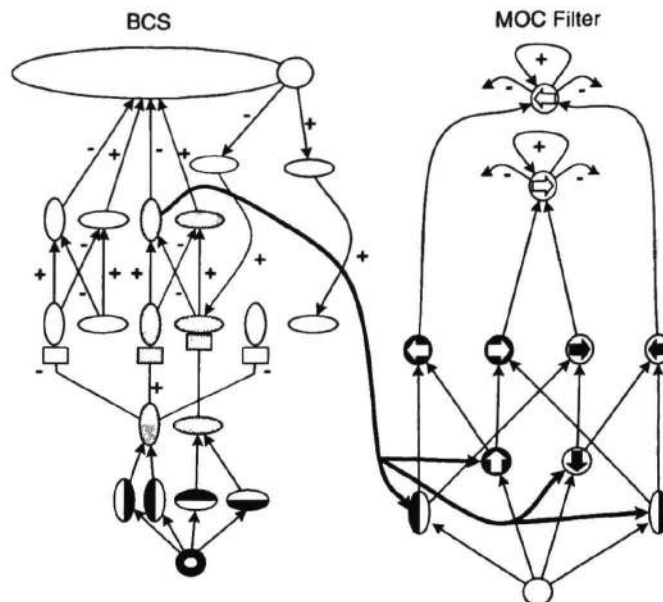

Figure 1: Form and motion integration. Oriented boundary signals in the BCS feed into like-oriented sustained cells and unoriented transient cells in the MOC Filter.

rows as the spatial separation between the flashes increases (Kolers, 1972; Neuhaus, 1930).

Boundary Contour System: Form processing

The Boundary Contour System (BCS), described in Grossberg & Mingolla (1985a,b), detects, completes, and regularizes boundary segmentations of a retinal image. Such segmentations can be defined by regions of different luminance or texture, or by illusory contours. These computations are carried out through a series of filtering, competitive, and cooperative stages as schematized in Figure 1.

The positive feedback between the cooperative bipole cells and the lower levels of hypercomplex cells of the BCS completes emergent boundary segmentations that coherently bind together appropriate feature combinations in the image (Grossberg, 1987). Such positive feedback also creates hysteresis which, in the absence of some compensatory reset mechanism, leads to undesirably long persistence times of boundary signals after stimulus offset (Grossberg, 1991).

Francis *et al.* (1993, 1994) showed that the dynamic characteristics of the BCS account for many percepts at stimulus off-

set, notably perceptually observed levels of visual persistence. The theory suggests that a key process governing visual persistence is the time taken to reset a segmentation. Hysteresis in the segmentation network corresponds to visual persistence, and the hysteretic properties of the BCS match psychophysical data on visual persistence, including inverse relations between persistence and target duration (Bowen, Pola, & Matin, 1974), greater persistence for illusory than real contours, and a nonmonotonic relationship between persistence and target duration for illusory contours (Meyer & Ming, 1988).

Motion Oriented Contrast Filter: Apparent motion

Grossberg & Rudd (1989, 1992) developed the Motion Oriented Contrast Filter (MOC Filter) to explain properties of motion and apparent motion. The MOC Filter computes local and global motion signals in a neural network through a sequence of excitatory and inhibitory connections. Figure 1 schematizes these interactions.

The model computes local directional motion signals by multiplicatively gating responses at oriented sustained cells and unoriented transient cells. Motion cells that are sensitive to short-range spatial interactions feed into cells that are sensitive to long-range spatial interactions. These latter cells have long-range Gaussian receptive fields that sample inputs from broad regions of the visual space. They also undergo strong lateral inhibition that suppresses all output except for the cell with the largest excitatory input. The competitive interactions of these cells create a continuously moving motion signal in response to the discreet flashes of an apparent motion display. Grossberg & Rudd (1989, 1992) correlated the properties of this traveling peak of activity with data on apparent motion.

Integration of form and motion

Grossberg (1991) suggested that a pathway connects BCS boundary signals to MOC Filter short-range motion signals to allow formation of motion percepts that are sensitive to perceived form and to help the motion system select the proper depth plane for a motion percept. Figure 1 shows such a linkage. In Figure 1, oriented boundary signals from the BCS feed into like-oriented sustained cells and unoriented transient cells in the MOC Filter that correspond to the same retinal location. Via this BCS-MOC Filter pathway, the MOC Filter becomes sensitive to spatiotemporal changes in form as well as to spatiotemporal changes in luminance. This additional sensitivity allows it to generate apparent motion signals in response to illusory contours and other visual segmentations. The following sections show how these properties explain the data described in the introduction.

Simulation of illusory contour apparent motion

Several authors have shown that illusory contours can move in apparent motion (Mather, 1988; Ramachandran, 1985; von Grünau, 1979). Grossberg & Mingolla (1985a,b) explained the formation of illusory contours as a special case of the boundary segmentation mechanisms needed to process visual forms. The generation of apparent motion between illusory contours requires signals from the form processing mechanisms into mechanisms responsible for generating apparent motion signals (Grossberg & Rudd, 1989, 1992). The model
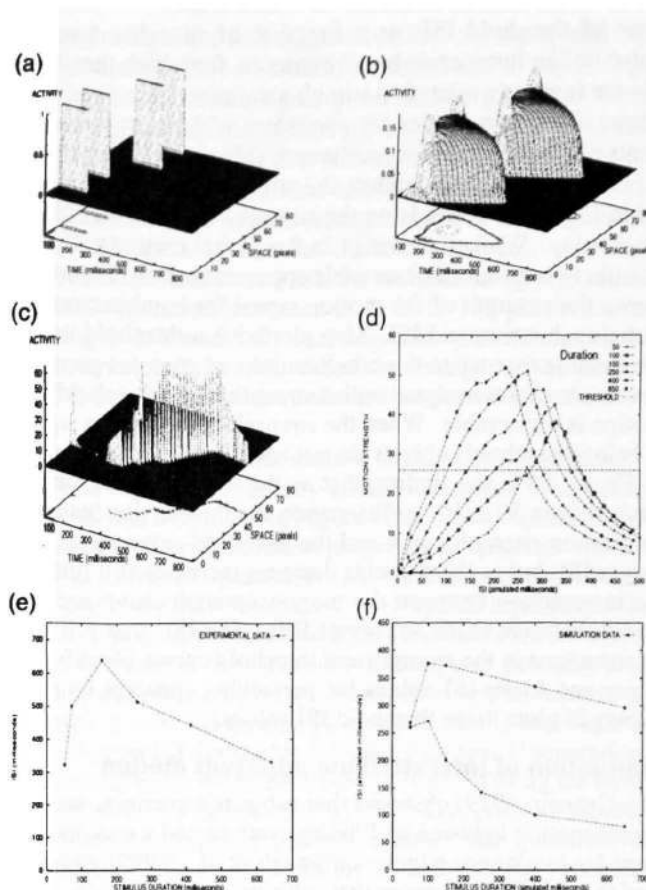

Figure 2: Computer simulation of illusory contour apparent motion. (a) Luminous inputs. (b) Boundaries produced by BCS. (c) Activity of global motion cells shows apparent motion. (d) Motion strength as ISI and stimulus duration changes. (e) Upper ISI thresholds for illusory contour apparent motion. (Replotted from Mather, 1988.) (f) Simulated upper and lower ISI thresholds.

interactions between form and motion mechanisms are sufficient to explain psychophysical data about apparent motion of illusory contours.

Figure 2 shows a simulation of illusory contour apparent motion. The inducing stimuli for a one-dimensional illusory contour consists of a pair of luminance increments (Figure 2a). The bipole feedback of the BCS completes a segmentation within the region defined by the two luminance increments (Figure 2b). This segmentation corresponds to the perceived illusory contour. Inputs from the BCS and from the luminous array feed into the MOC Filter. A plot of the activity of global motion cells through time shows motion from the first illusory contour to the second (Figure 2c).

Mather (1988) investigated the temporal properties of illusory contour apparent motion. Figure 2e replots data from Mather (Figure 5, subject PG), and shows the upper ISI values for which subjects report seeing apparent motion between two illusory Kanizsa squares as a function of the inducing stimuli duration. The upper ISI threshold values for these illusory contours is larger than that of corresponding luminance-based contours (as described below). Moreover, the inverted-U

shape of threshold ISIs as a function of stimulus duration is also unlike luminance-based contours, for which threshold ISIs are inversely related to stimulus duration (also described below). These properties are consistent with direct measurements of illusory contour persistence (Meyer & Ming, 1988).

For fixed spatial separation, the strength of the motion signal in Figure 2c depends on the stimulus duration and ISI of the display. Weaker activities in the global motion cells are less likely to produce observable apparent motion. Figure 2d shows the strength of the motion signal for combinations of stimulus duration and ISI. Also plotted is a threshold value. We assume that when the combinations of stimulus parameters create a motion signal with a strength above threshold, the motion is observable. When the strength of the motion signal is below threshold subjects do not see it. A critical property of Figure 2d is the finding that as the stimulus duration increases from 50 to 100 milliseconds, the intersection between the motion strength curve and the threshold curve shifts to a longer ISI; but as the stimulus duration increases still further, the intersection between the motion strength curve and the threshold curve shifts to shorter ISIs. The ISIs that produce intersections in the strength and threshold curves identify the upper and lower ISI values for perceiving apparent motion. Figure 2f plots those threshold ISI values.

Simulation of interattribute apparent motion

Von Grünau (1979) observed that subjects sometimes see apparent motion between an illusory contour and a contour defined by luminance edges. Cavanagh *et al.* (1989) generalized this result by showing that subjects report seeing motion between stimuli defined by any combination of attributes, including: luminance, color, texture, relative motion, or stereopsis. They noted that motion between stimuli of different attributes is weaker than motion between stimuli of the same attribute.

The ability to see apparent motion between stimuli of different attributes is consistent with the properties of form and motion integration described in this paper. Figure 3a shows luminous inputs for an interattribute simulation. The first stimulus is a pair of illusory contour inducers and the second stimulus is a luminance edge. Figure 3b shows the boundary signals produced in the BCS to the inducers and the luminous contour. Figure 3c shows the resulting activity of global motion cells in the MOC Filter (points are sampled more frequently to catch all the motion). The activity shifts from the location of the illusory contour to the location of the luminous stimulus. This simulation demonstrates interattribute apparent motion.

The BCS segments stimuli of many different attributes, including: illusory contours (Grossberg & Mingolla, 1985a), textures (Grossberg & Mingolla, 1985b), luminance (Grossberg & Todorović, 1988), and stereopsis (Grossberg, 1994; Grossberg & Marshall, 1989). The integration of form and motion offers a consistent explanation of many types of interattribute apparent motion by suggesting that these segmentations feed into the MOC Filter, which generates the apparent motion percept.

Simulation of Korte's laws

The previous two sections demonstrate that integrating percepts of form and motion explains complicated dynamic prop-
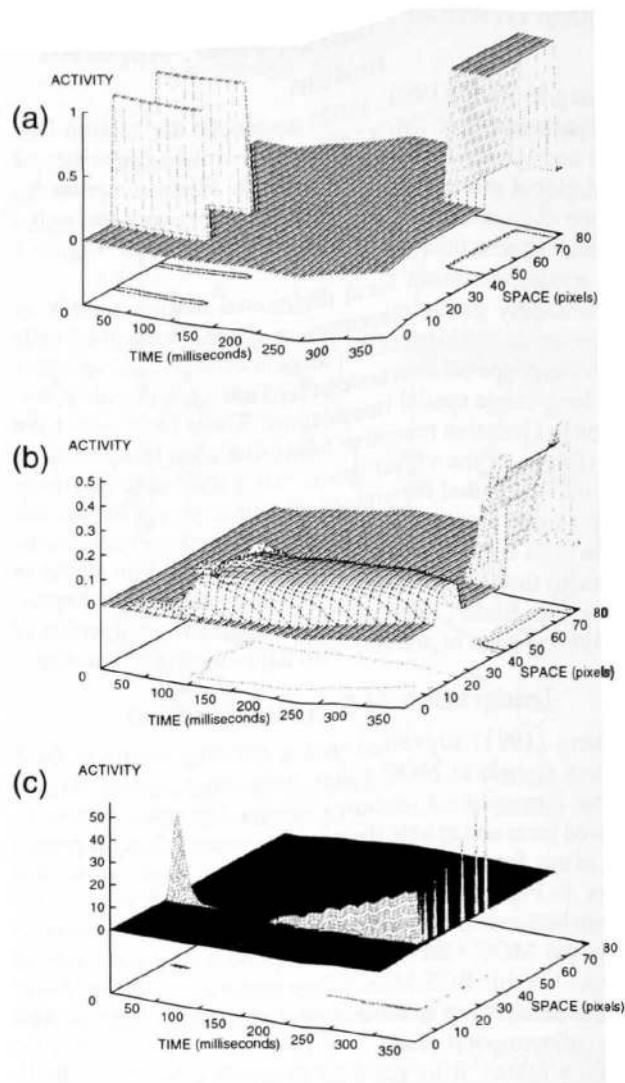

Figure 3: Computer simulation of interattribute apparent motion. (a) Luminous inputs. (b) Boundary signals produced by the BCS. (c) Activity of global motion cells shows apparent motion.
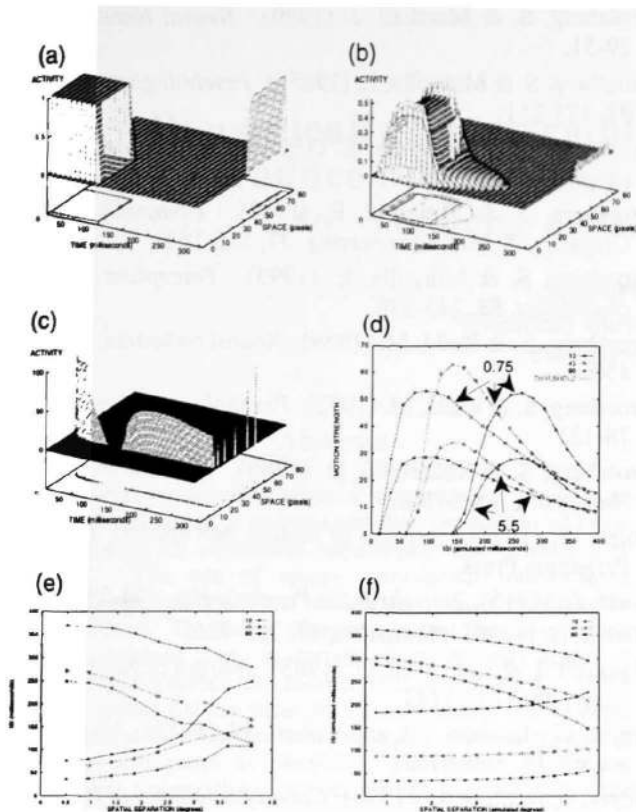
Figure 4: Computer simulation of apparent motion between luminous stimuli. (a) Luminous input. (b) Boundary signals produced by the BCS. (c) Activity of global motion cells shows apparent motion. (d) Motion strength as a function of ISI, stimulus duration, and spatial separation. (e) Psychophysical upper and lower ISI thresholds (Replotted from Kolers, 1972; after Neuhaus, 1930). (f) Simulated upper and lower ISI thresholds.

erties of apparent motion that depend on visual form. This section shows that the dynamic properties of form perception are also relevant to stimuli that do not obviously require form processing for motion detection.

Figure 4a shows the inputs for a standard apparent motion display, the stimuli are luminance edges separated in space and time. Figure 4b shows the response of boundary signals to the luminous stimuli. Figure 4c shows the resulting activities of global motion cells. The moving activity corresponds to a percept of apparent motion.

Figure 4e shows psychophysical upper and lower ISI threshold values for apparent motion of luminance-based stimuli (Kolers, 1972 after Neuhaus, 1930). This figure shows that as stimulus duration increases from 10 to 45 to 90 milliseconds, each upper and lower ISI threshold curve decreases at every spatial separation. Moreover, as the distance between the two stimuli increases, the range of ISIs that produce apparent motion narrows, with the upper ISI decreasing and the lower ISI increasing for every stimulus duration. These properties are similar to Korte's laws (Korte, 1915).

The lag time of the local motion responses across all cells to the first stimulus offset, the duration of the response for

the same cells to the first stimulus offset, and the spatial separation between the two stimuli all contribute to the strength of the apparent motion signal generated by the MOC Filter. Figure 4d plots the strength of the motion signal, generated from offset signals of the first stimulus to onset signals of the second stimulus, as a function of ISI, spatial separation, and flash duration. The motion strength curve is shifted toward smaller ISI values as stimulus duration increases. Also, for fixed stimulus duration and ISI, the motion strength decreases as spatial separation increases from 15 to 110 pixels (corresponding to 0.75 and 5.5 visual degrees). Also plotted is the motion strength threshold. When the strength of the motion signal is below threshold we assume subjects do not observe it.

The intersections of the motion strength threshold with a motion strength curve identify the ISI thresholds. The points of intersection are plotted in Figure 4f and show that the model captures all the key qualitative properties of Neuhaus' (1930) results as well as the quantitative 350 millisecond gap between upper and lower ISI thresholds at small spatial separations. In particular, both upper and lower ISI thresholds are inversely related to stimulus duration, and the range of ISIs that produce apparent motion percepts narrows as spatial separation increases. Lower ISI thresholds increase with spatial separation and upper ISI thresholds decrease with spatial separation. All the simulations of the BCS were performed using the same parameters as in Francis et al. (1994). Our goal in this article is to demonstrate key qualitative, rather than quantitative, relationships. The approximations that are necessary to make the simulations computationally feasible do not yet warrant a search for optimal parameters.

Conclusions and predictions

While this paper focuses on simulations of psychophysical data, there exist neurophysiological data that support our hypothesis concerning form and motion integration. Motion (Albright, Desimone & Gross, 1984; Maunsell & van Essen, 1983; Mikami, Newsome & Wurtz, 1986a) and apparent motion (Mikami, Newsome & Wurtz, 1986b; Newsome, Mikami & Wurtz 1986) are believed to be processed in area MT of visual cortex. MOC Filter model analogs have been identified in area MT (Grossberg & Mingolla, 1993; Grossberg & Rudd, 1989, 1991). Von der Heydt, Peterhans & Baumgartner (1984) reported evidence that area V2 processes the emergent segmentations that underlie visual form using neural analogs of the BCS bipole cells. Neurological evidence for other parts of the BCS in area V2 and V4 is reviewed in Grossberg (1987). The form and motion interactions described in this paper are predicted to be realized as a neural pathway from area V2 (or V4) to area MT. Such pathways do exist (DeYoe & van Essen, 1988).

Grossberg (1991) describes a method of testing whether the V2 to MT pathway plays the role suggested in this article. An experimenter could train a monkey to respond when it sees apparent motion of illusory contours. A (reversible) lesion of area V2 or the V2 → MT pathway should abolish the percept and the response.

The theory makes strong psychophysical predictions as well. When the duration of the BCS response to a stimulus establishes the upper ISI threshold, then the stimulus properties

that favor longer visual persistence should also favor longer upper ISI thresholds for apparent motion. This relationship predicts a result that can support the role of the BCS-MOC Filter pathway in establishing upper ISI thresholds. Meyer, Lawson and Cohen (1975) showed that adaptation to an oriented grating influences the persistence of a subsequent test grating in an orientation-specific manner. When the orientation of the adaptation and test grating are orthogonal, persistence of the test grating increases, relative to the no-adaptation case. Francis *et al.* (1994) simulated this property with the BCS model.

If persistence of boundary signals sets the upper ISI threshold of apparent motion, then, other things being equal, adaptation to a grating should increase the upper ISI threshold for apparent motion of an orthogonally oriented grating. In the BCS, the increase in persistence is due (in part) to competition between hypercomplex cells that are tuned to orthogonal orientations at the second competitive stage (Figure 1). The MOC Filter does not include a stage of competition between orthogonal orientations. Instead, competition occurs between opposite *directions* of motion, which differ by 180°, not 90°, thereby giving rise to motion contrast cells (Grossberg, 1991). Thus, the luminance-based pathway of the MOC Filter should not contribute to a change in the upper ISI threshold after adaptation. Such a change in the upper ISI threshold can, however, be explained by BCS–MOC Filter interactions. More generally, stimulus features that change the duration of visual persistence should tend to have a similar effect on upper ISI thresholds of apparent motion.

Acknowledgements

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