A computational and perceptual account of motion lines

Hyungjun Kim, Gregory Francis
Department of Psychological Sciences, Purdue University, 1364 Psychological Sciences Building,
West Lafayette, IN 47907-1364, USA; e-mail: gfrancis@psych.purdue.edu
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Abstract. To indicate motion in a static drawing, artists often include lines trailing a moving object. The use of these motion lines is notable because they do not seem to be related to anything in the optic array. We analyze the dynamic behavior of a neural network model for contour detection and show that it generates trails of oriented responses behind moving stimuli. The properties of the oriented response trails are shown to correspond to motion lines. The model generates trails of different orientations depending on the speed and length of the movement, and thereby predicts different uses of two types of motion lines. The model further predicts that motion lines should bias real motion in some situations. An experiment relating motion lines to ambiguous motion percepts demonstrates that motion lines contribute to motion percepts.

1 Introduction

Many cues convey an impression of movement in static images. Even without seeing literal movement a viewer can have the sense of seeing a snapshot of something that was moving. Some cues to motion in static images arise from their correlation with true moving objects. For example, a snapshot of a child jumping in midair conveys a strong sense of motion because the viewer knows that masses must be pulled back down toward the ground by the Earth's gravity (Freyd, 1992). Likewise, when objects move they can take postural positions very different from objects that are nonmoving. Friedman and Stevenson (1975) and Carello, Rosenblum, and Grosofsky (1986) demonstrated that such posture cues influence judgments of implied motion in static images.
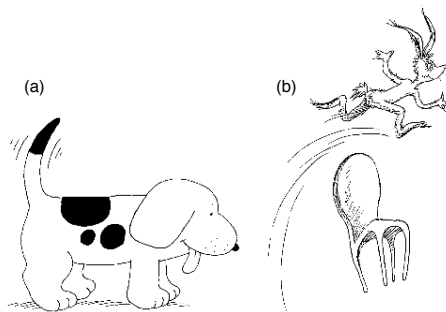

Figure 1: Examples of motion lines. (a) When lines are drawn on either side of an object and have the same orientation as the object, the impression is that the object is moving rapidly back and forth. (Reprinted from *Where's Spot?* by E. Hill, 1980.) (b) When lines are drawn to one side of an object and have an orientation orthogonal to the object, the impression is that the object is moving along a path indicated by the lines. Cues such as posture and position also contribute to the impression that the creature is moving. (Reprinted from *The foot book* by Dr. Seuss, 1968.)

Other drawn indicators of motion seem unrelated to percepts of moving objects. One pictorial device is to draw trailing lines (called motion lines, speed lines, or action lines) behind a moving object. Figure 1a reprints a drawing where wagging of a dog's tail is indicated by lines on either side of the tail. Lines parallel to the contours of a quickly moving object are often used to indicate vibration. Figure 1b shows a different type of motion line. Here the path of motion of a character jumping over a chair is indicated by the presence of motion lines drawn parallel to the trajectory of motion. Motion lines of both sorts are ubiquitous in comic books, children's books, and logos of all sorts. Motion lines are not a Western or modern creation; they have also been found in 11th century Japanese drawings (Friedman & Stevenson, 1980) and in sketches of Leonardo da Vinci (Koenderink, 1985).

There is experimental evidence that motion lines are effective cues to motion in static images. Friedman and Stevenson (1975) found that motion lines influenced childrens' judgements of movement in still pictures. Brooks (1977) found that the presence of motion lines influenced childrens' memories for pictures with implied motion. Carello *et al.* (1986) found that motion lines play a significant role in the judgment of implied speed in static images.

Motion lines seem unique among pictorial conventions for implied motion because there is nothing in the optic array that corresponds to motion lines (Hagen & Jones, 1978). When objects move in the physical world they do not leave a trail of lines in the air behind them. While it is true that fast moving stimuli leave a blur trail (Burr, 1980), the resulting percept is blurry all over and not like motion lines (see the photograph in Burr, 1980). Because of a lack of any part of the optic array with which to link motion lines, they are often classified as a metaphorical pictorial device. Kennedy (1982) suggested that motion lines are ecological in certain cases. Examples of ecological validity include a cart leaving tracks, a water fowl leaving a wake on a lake, and a cloth clearing a path on a dusty surface. Kennedy suggested that path-of-movement indicators are literal or perceptual when left on surfaces and metaphorical when they appear in empty space, as with motion lines. Friedman and Stevenson (1975, 1980) raised similar arguments.

We propose a very different account of motion lines. While it is true that the optic array has no correlate to motion lines, we suggest that at a specific level of neural coding moving stimuli generate responses that are related to motion lines. Through analysis of a neural network model of visual perception we suggest that the vibration marks in Figure 1a correspond to persisting representations in a network coding stimulus contours. The same analysis suggests that path-of-movement motion lines, as in Figure 1b, correspond to cortical afterimages generated by offset of contours. The neural mechanisms underlying these network properties are summarized in the next section.

2   Boundary Contour System

The model, called the Boundary Contour System (BCS), consists of a large set of individual neurons that are linked by excitatory and inhibitory connections to promote computations necessary for visual perception. Since Grossberg (1994) recently reviewed the BCS model and described its relations to other parts of visual perception and to parts of visual cortex, this paper will only describe the model in general terms. The BCS' functional purpose is to identify the location and orientation of stimulus edges or boundaries. It accomplishes this by first feeding a visual image to simple cells, each with a receptive field tuned to changes in luminance at a specific location and orientation. Signals from these cells contribute to complex cells that become insensitive to the direction of luminance change, but remain sensitive to orientation and position. These complex cells then feed into a series of cooperative and competitive stages that selects a consistent pattern of cell activations coding location and orientation of stimulus boundaries.

A key component of this identification process is the use of excitatory feedback. The equilibrium response of the network will mostly include cells that send positive feedback to each other (directly or indirectly). Cells within an active excitatory feedback loop are said to have activities that resonate. Among other properties, this type of feedback allows the network to complete broken contours that occur due to shadows of retinal veins or other types of noise. Grossberg and Mingolla (1985) showed that this excitatory feedback improves the network's ability to process spatial information.

The benefits of excitatory feedback for spatial processing come at a cost for temporal processing. The resonance generated by excitatory feedback loops dominates the temporal properties of the BCS. Simulations
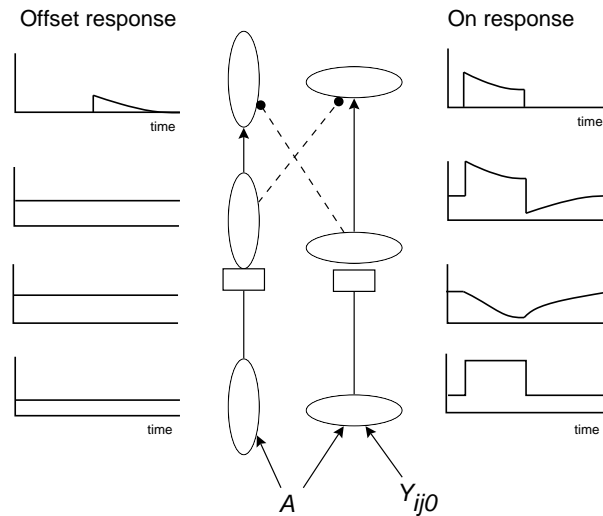
Figure 2: At stimulus offset, a gated dipole circuit produces a transient rebound of activity in the non-stimulated opponent pathway. When the pathways code opposite orientations, offset of a horizontal input leads to a rebound of vertical activity. Dashed lines with circle terminators indicate inhibition, solid arrows indicate excitation, boxes indicate transmitter gates. The plot next to each cell or gate schematizes the signal strength over time as a horizontal input is applied and removed. Offset of the horizontal input leads to a rebound of activity in the vertical pathway.

in Francis, Grossberg and Mingolla (1994) demonstrated that, if left unchecked, resonating signals can last for hundreds of simulated milliseconds. To prevent resonating signals from lasting indefinitely, internal processes in the network automatically speed disappearance of persisting neural signals. Francis *et al.* (1994) identified two mechanisms embedded in the BCS design that reset activities in the feedback loop. One is lateral inhibition, and the other is a reset mechanism that inhibits persisting signals. The properties of lateral inhibition account for and predict many characteristics of visual masking, including effects on visual persistence (Francis *et al.*, 1994; Francis, 1996a), temporal integration (Francis, 1996b), and metacontrast masking (Francis, 1997).

The reset mechanism derives from a different set of mechanisms. Figure 2 schematizes separate pathways sensitive to the same position in visual space but perpendicular orientations. These pathways compete via reciprocal inhibition from lower levels to higher levels. Feeding this competition are inputs gated by habituative transmitters. Along with signals from external stimuli, each input pathway receives a tonic source of activity, and all output signals are rectified. This combination of rectification, opponent competition, habituative transmitter gates, and tonic input creates a gated dipole circuit. At the offset of stimulation, a gated dipole circuit generates a transient rebound of activity in the previously non-stimulated pathway.

The time plot next to each cell or gate describes the dynamics of this circuit. In the case shown, the sharp increase and then decrease of the time plot at the lower right of Figure 2 indicates that an external input stimulates the horizontal pathway. In response to the stronger signal being transmitted to the next level, the amount of transmitter in the gate inactivates, or habituates, during stimulation and then rises back toward the baseline level upon stimulus offset. Notice that the inactivation and reactivation of transmitter occurs more slowly than changes in the activities of the neural cells. Each slowly habituating transmitter multiplies, or gates, the more rapidly varying signal in its pathway, thereby yielding net overshoots and

undershoots at input onset and offset, respectively. During stimulation, the horizontal channel wins the rectified opponent competition against the vertical channel as indicated in the top right time plot. However, upon offset of the stimulation to the horizontal channel, the input signal returns to the baseline level but the horizontal transmitter gate remains habituated below its baseline value. As a result, shortly after stimulus offset, the gated tonic input in the horizontal channel has a net signal below the baseline level. Meanwhile, the vertical pathway maintains the baseline response at all cells and gates before the opponent competition. Thus, when the horizontal channel is below the baseline activity, after stimulus offset, the vertical channel wins the rectified opponent competition and produces a rebound of activity as shown in the top left time plot. As the horizontal transmitter gate recovers from its habituated state, the rebound signal in the vertical channel weakens and finally disappears. The duration of the transient rebound thus matches the recovery rate of the transmitter from habituation.

The top level of the gated dipole circuit contributes to another circuit that determines the location and orientation of stimulus boundaries using positive feedback. In these neural circuits, an orientationally sensitive cell is excited by cells of the same orientation sensitivity and inhibited by cells of the orthogonal orientation sensitivity. Thus, the rebound generated by the gated dipole circuit inhibits any persisting activity generated by the oriented edges of the stimulus.

The properties of reset signals explain why persistence of static stimuli varies inversely with stimulus luminance and duration (e.g., Bowen, Pola & Matin, 1974), and why the persistence of illusory contours is greater and differently affected by stimulus duration than luminance contours (Meyer and Ming, 1988). In each case, stimuli that produce a strong response among oriented cells feeding into the gated dipole generate a strong reset signal at stimulus offset. The strong reset signal greatly reduces persistence. Weaker stimuli (smaller luminance, shorter duration, fewer luminance contours) produce weaker reset signals at stimulus offset, thereby allowing persisting neural signals to last longer. Details of these model properties are in Francis *et al.* (1994).

Signals in the BCS are insensitive to direction of contrast, and thereby are similar to concepts of visual form. Groupings of BCS activities can be recognized as corresponding to specific shapes, without requiring associated percepts of brightness or color (Grossberg & Mingolla, 1985). The boundary signals in the BCS interact with a complementary system called the Feature Contour System (FCS), which codes brightness and color information. Activities in the FCS diffuse across surfaces until constrained by boundaries from the BCS (Grossberg & Todorović, 1988).

Francis and Grossberg (1996) noted that the properties of a type of afterimage support the existence of reset signals used in the BCS. MacKay (1957) reported an orientation afterimage that appears after viewing a set of radial lines, passing through a common center point , for several seconds and then looking at a blank screen. The afterimage consists of a perceived wavy circular form. Similarly, viewing a set of concentric outline circles produces a radially organized afterimage. The afterimage often does not include brightness or color, but conveys only an impression of form or shape. Francis and Grossberg simulated the BCS model and showed that the spatial organization of rebound signals generated by the offset of stimuli of this sort are grouped together to produce these types of orientation afterimages.

3   Motion lines

In this section we analyze the dynamic responses of the BCS to moving stimuli. We show that the BCS's representation of contours corresponds to various types of motion lines. In the model, a moving stimulus generates a trail of responses among orientationally tuned cells. We suggest that some unspecified mechanism of the visual system interprets these patterns of oriented activities as cues to motion. A nonmoving stimulus with drawn motion lines will excite many of the same cells. Thus, motion lines convey an impression of motion in a static image by tapping in to systems that are tuned to those cues for motion.

3.1   Vibration marks and persistence

While the mechanisms described in the previous section shorten the duration of persisting signals in the BCS, a fast moving stimulus will leave a trail of persisting responses that code the orientation of the stimulus.
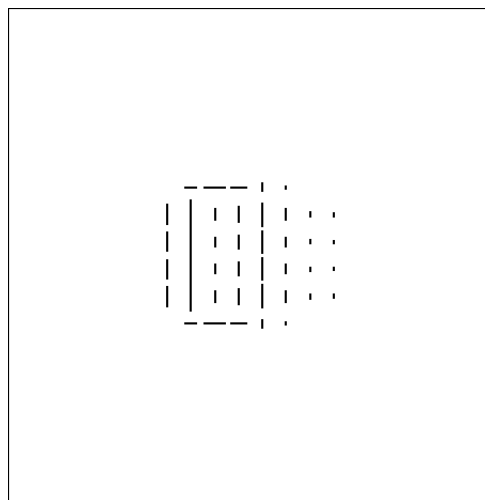
Figure 3: A simulation demonstrating persistence of oriented responses in the model. The stimulus was a vertically oriented bar that moved two pixels to right, four pixels to the left, and then two pixels to the right to stop in the center of the image plane. Movement of the bar leaves a trail of persisting vertical signals that are similar to the vibration marks in Figure 1a.

Figure 3 summarizes a simulation that shows this effect. The equations governing the simulations are described in the Appendix. In the simulation a $(4 \times 6$ pixel) luminous bar started at the middle of the image plane and then shifted two pixels to right, four pixels to the left, and then two pixels to the right, so that it ended at the same place it started. The bar moved quickly, relative to the dynamics of the equations; spending one time unit at each pixel location. Figure 3 shows the responses of all cells when the bar reaches its resting place.

This snapshot demonstrates significant temporal-spatial interactions. The strongest responses outline the edges of the stimulus, when it was shifted one pixel to the left of center. These responses are persisting representations. The responses to the bar at the center, where it is physically located, have not, at the time of the snapshot, grown as strong as the persisting responses. Signals to the left and right of the center are also persisting responses that coded the vertical edges of the stimulus.

We propose that the type of motion lines used in Figure 1a to indicate vibration correspond to the persisting representations of contour information in the BCS. Significantly, we note that motion lines used to indicate short, quick movements like in Figure 1a utilize lines that have the same local orientation as the moving stimulus. This characteristic is consistent with the proposal that such motion lines schematize the persisting oriented responses generated by quickly moving stimuli.

It should be noted that the persisting representations in Figure 3 do not directly correspond to blurred percepts generated by fast moving stimuli. In the general theory, percepts of smeared brightness must correspond to FCS activities, as the BCS activities do not code brightness percepts. This distinction is emphasized because one could imagine a model-neutral explanation that hypothesizes that vibration marks are schematic drawings of blur. While the model predicts that blur is strongly associated with moving stimuli that generate persisting BCS responses, it further suggests that the vibration marks are schematics of the BCS responses and not the blur *per se*. This model property explains why cues for vibration consist of drawn lines instead of smears of color, which would seem better representations of perceived blur.

3.2 Path-of-movement lines and reset signals

Figure 4 shows responses generated by the model simulation when the bar stimulus moves across the image plane more slowly (4 time units per pixel) than in Figure 3. Figure 4a shows the responses generated by the bar before any movement. The oriented signals outline the bar luminance edges. Figure 4b shows

the oriented responses after the bar has moved halfway across the image plane. In addition to the strong responses along the luminance edges, rebound signals produce a trail of responses at the previous locations of the bar. The inset magnifies the responses in the indicated box to better show the orientation sensitivity of the cell responses. In the inset, the vertical lines represent persisting responses from vertical cells that responded to the moving vertical edge. The horizontal responses correspond to the reset signals generated in the gated dipole circuit at the offset of the vertical response. Figure 4c shows the responses when the bar has moved all the way across the image plane. A long trail of horizontal orientation afterimages remains.

The reset signal trail contains information about the stimulus' movement. The relative strength of responses within a trail provides information about the direction of motion. Close inspection of the inset in Figure 4c shows that the oriented responses decrease in magnitude with separation from the stimulus edge. This occurs because reset signals farther away from the stimulus have had more time to decay. The speed of a stimulus is partly coded by the length of its reset signal trail. As comparison of Figures 5a (fast) and b (slow) indicates, a faster stimulus leaves a longer reset signal trail because it moves a greater distance before the signals decay away. The length of the trail can also be influenced by the luminance of the stimulus, with more luminous stimuli producing stronger afterimages and longer trails.

Figure 5c shows the responses from a horizontal cross-section of reset signal responses generated by the fast and slow moving stimuli in Figures 5a and b. Responses are plotted at the time that the trailing edge of the stimulus moves off position 13 to position 14 as it translates across the image plane. The dashed line indicates a fixed threshold that was applied to the responses for producing Figures 5a and b. The rebound responses generated by the fast stimulus remain above the threshold during the movement of the bar, while the responses generated by the slow stimulus have decayed below threshold for the small pixel locations (where the movement started).

The key difference between the responses of the fast and slow stimuli is the time necessary to traverse the image plane. The fast stimulus remains at each pixel location for 4 time units, while the slow stimulus remains at each pixel location for 8 time units. As a result, it takes the slow stimulus twice as long to move across the image plane. Thus, the rebound signal generated by the slow stimulus at pixel 1 has decayed for twice as long as the signal generated by the fast stimulus at the same location. This time difference generally means that the response from the fast stimulus is larger than the response from the slow stimulus. An exception is at pixel 13, which is the position each stimulus just moved off. Here, the response from the fast stimulus is smaller because of two factors. First, there remains some persisting activity in the vertical pathway, which limits the response in the horizontal pathway. Such persisting activity has decayed at pixel 12, which explains why the strength of the rebound is stronger at pixel 12 than at pixel 13 for the fast stimulus. Second, the slower stimulus remains at each pixel position for twice as long as the fast stimulus. As a result it more fully habituates the transmitter gates in the gated dipole, and generates a stronger rebound at stimulus offset. Thus, the initial strength of the rebound is larger for the slow stimulus than for the fast stimulus. This advantage is quickly eroded, though, as the responses from the slow stimulus decay before the stimulus moves very far.

The spatial layout of the reset signal trail suggests the path of movement of the stimulus. In Figure 5d the vertical bar moves from the lower left to the upper middle to the lower right. The distribution of reset signals indicates the trajectory of the bar. As the inset shows, the pattern of oriented responses in the reset signal trail include both vertical and horizontal signals. The horizontal (vertical) signals correspond to reset signals generated by the vertical (horizontal) edges of the stimulus.

We propose that the type of motion lines used in Figure 1b to indicate path of movement correspond to the trail of reset signals generated in the BCS by a moving stimulus. Consistent with this hypothesis is the observation that path-of-movement motion lines are drawn with orientations that are generally orthogonal to the orientation of the moving stimulus.

4   Motion lines and motion percepts

We suggest that motion lines tap into neural mechanisms that treat trailing contour signals as cues to motion. Such contour trails are created, in the model circuits, in response to moving stimuli. If such trails are cues to perceived motion it is reasonable to wonder why artists' rendering of motion lines do not convey a percept of
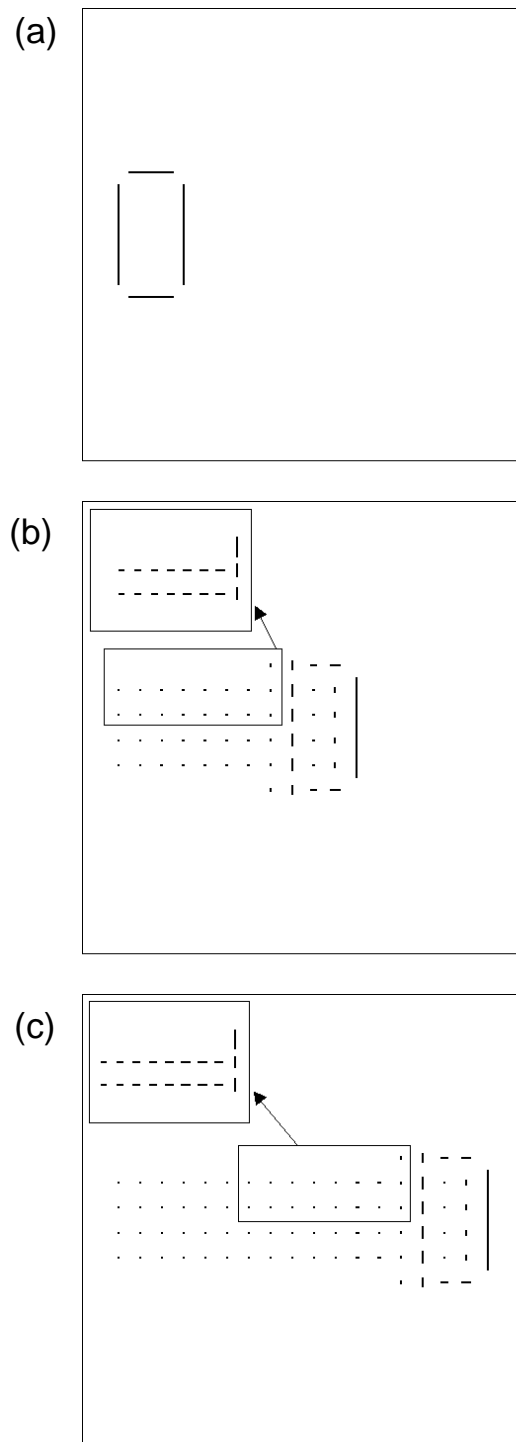
Figure 4: Simulations demonstrating the generation of oriented rebounds trailing a moving vertical bar. (a) Orientation responses before the stimulus moves. (b) Orientation responses when the bar has moved half way across the image plane. In addition to the responses outlining the luminance changes, rebound responses indicate the path of movement. (c) A trail of oriented rebound signals is similar to the motion lines in Figure 1b.
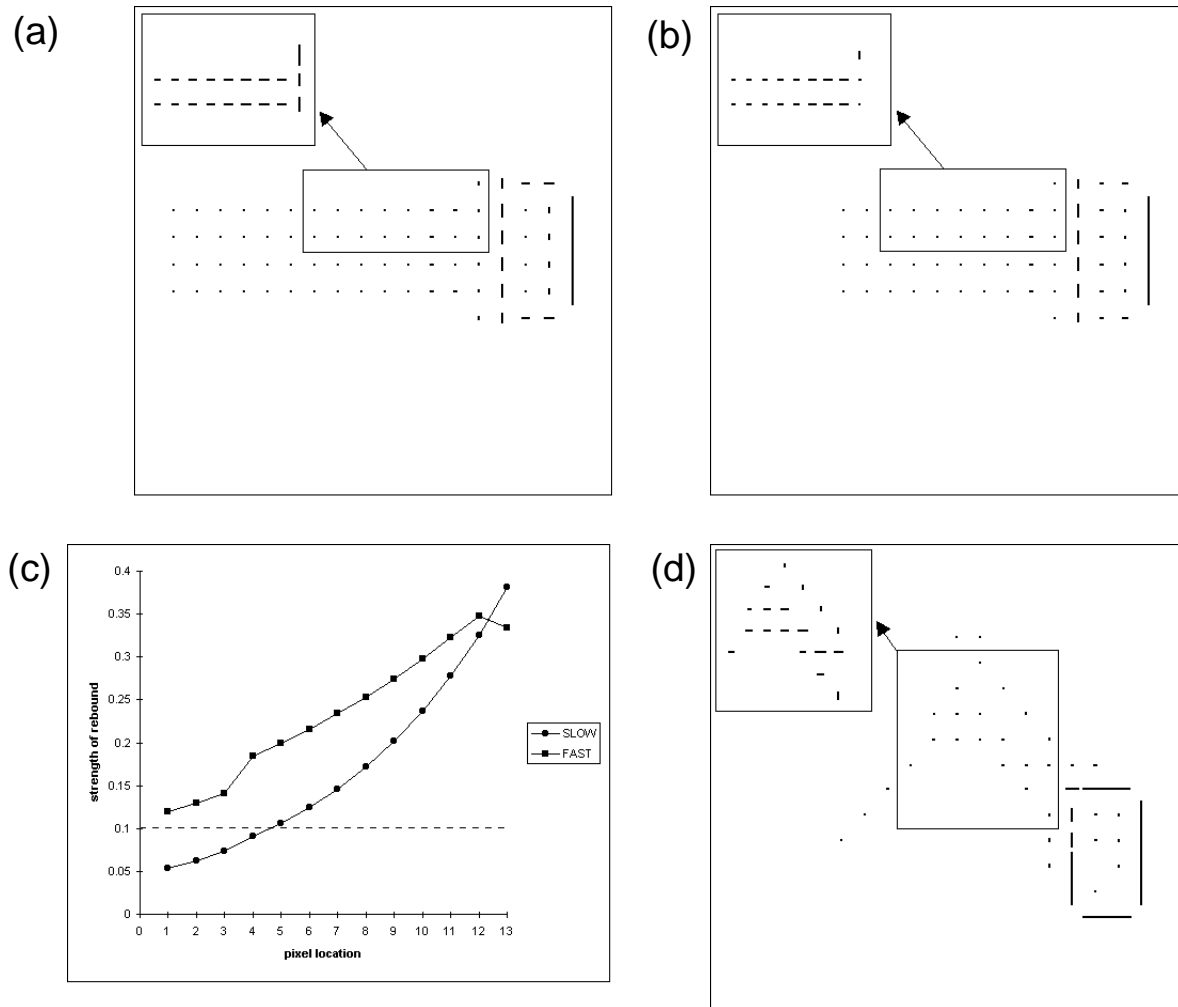
Figure 5: Simulations demonstrating rebounds generated by a moving vertical bar. (a) Rebounds generated by a fast moving bar. (b) When the moving bar travels at half the speed, it leaves a shorter trail because the rebounds decay further before the bar reaches the end of the image plane. (c) Rebound responses along a cross section of the image plane for the fast and slow stimulus. (d) When the bar moves from the lower left to the upper middle to the lower right of the display it leaves a path of orientation rebounds that indicates its trajectory.
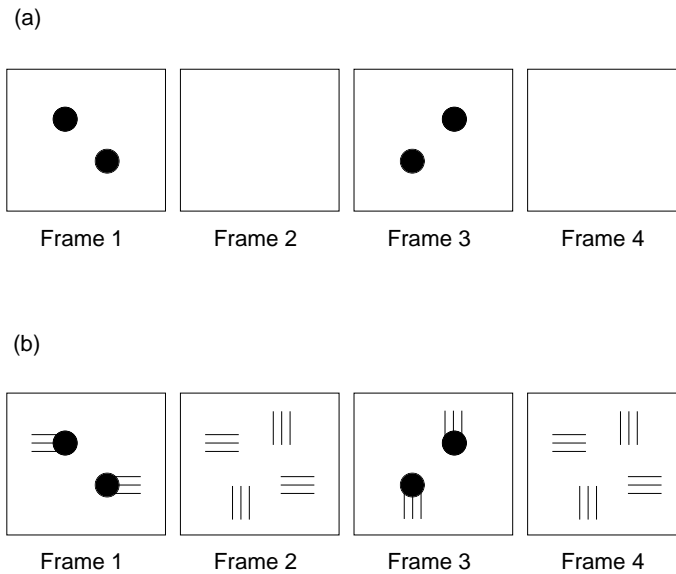
(a)

(b)

Figure 6: A schematic of the stimuli used in the experiment. On the monitor, the stimuli were white on black (a) The standard bistable motion display. When set in a continual loop, observers generally report seeing horizontal or vertical motion. (b) When motion lines are added to the display the model predicts that observers should see clockwise rotation of the dots. On the monitor the motion lines were more numerous and thinner.

true motion, rather than an implication or understanding of motion, as is typically observed. We suspect the answer consists of at least two parts. First, from a model-neutral point of view, there may be many different contributions to motion percepts. We hypothesize that for real moving objects, motion lines contribute to, but do not solely determine, the accompanying motion percept. In a static image with drawn motion lines, the other cues to motion are absent, and cues for stationarity may conflict with the implications of motion lines.

Second, the model proposes a distinct difference between drawn motion lines and oriented trails generated by moving stimuli in the BCS. As mentioned previously, the BCS interacts with a complementary system called the FCS, whose activities code information on brightness, color, and other surface properties. The oriented trails (especially those generated by reset signals) are unlikely to correspond with any FCS representations, as the color and brightness of a moving stimulus is trapped by the boundaries of the stimulus itself. In contrast, the motion lines used to imply motion in a static drawing necessarily generate both BCS orientational and FCS brightness responses. The extra responses in the FCS may preclude the BCS orientational information from acting as a strong cue to motion.

4.1   Experiment

Despite these caveats, the model generally predicts that motion lines *should* influence percepts of real moving objects. We tested whether path-of-movement motion lines biased motion percepts in an ambiguous motion display. When presented with the repeating sequence of frames in Figure 6a, observers report seeing apparent motion between the dots in Frame 1 and the dots in Frame 3. Observers' percepts tend to be of two types. Either they consist of vertical movement for both the left and right dots, or they consist of horizontal movement for both the top and bottom dots. These are mutually exclusive percepts, observers report seeing either vertical or horizontal, but not both at once. The percepts are often bistable, with frequent changes between horizontal and vertical motion directions. Although they are reported less frequently, it is also possible to see the dots moving in clockwise or counterclockwise directions.

The experiment explores how the presence of motion lines biases observers to report motion directions
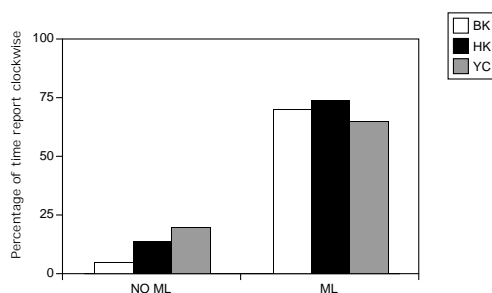
Figure 7: Percentage of time observers reported seeing clockwise rotation of the dots. For the no motion line condition, clockwise rotation was rare. For the motion line condition, clockwise rotation was frequently observed.

consistent with the directions implied by the motion lines. We designed ambiguous motion displays to include motion lines that, if used, would disambiguate the overall motion organization.

4.1.1   Methods

Observers
Three observers with normal or corrected to normal vision participated in three sessions each. One observer was an author, the other two were naive to the purpose of the study.
Display
All stimuli were presented on a Silicon Graphics Indy computer. Figure 6 demonstrates the type of stimuli used in all the experiments. Figure 6a schematizes the standard stimulus. Frame 1 included two dots on opposite corners of an imaginary square. Frames 2 and 4 were blank screens. Frame 3 included two dots on opposite corners of an imaginary square, but the corners not used in Frame 1. The frames were presented in a loop so that frame 1 appeared right after frame 4. The percept was of dots moving, usually back and forth either horizontally or vertically.

The dots were circles with a radius of 1.08 deg. The center-to-center distance of a dot from frame 1 to frame 2 was 5.56 deg. The dots had a luminance 52 cd/m^2 and the background was 0.06 cd/m^2. Each frame was presented for 150 milliseconds.

The motion line stimulus is schematized in Figure 6b. It was identical to the standard stimulus except motion lines were added to various frames. Frame 1 added motion lines to the left and right sides of the dots, thereby implying horizontal movement. Frame 2 added motion lines to the top and bottom sides of the dots, thereby implying vertical movement. Motion lines were also added in all positions for frames 2 and 4. Each set of motion lines consisted of nine lines, with a length of 5.40 deg, thickness of 0.077 deg, and luminance of 5 cd/m^2.
Procedures
In each trial, an observer viewed a repeating sequence of images in Figure 6a or b for thirty seconds. The observer noted, by keypresses, whenever the percept changed to or from clockwise motion. The computer kept track of the time that an observer saw clockwise motion. Observers first went through five practice trials each with and without motion lines. Data was then gathered from ten trials without motion lines and ten trials with motion lines; which were randomly mixed as the observer went through a testing session.

4.1.2   Results

Figure 7 plots the percentage of time that each observer reported seeing clockwise motion for each stimulus type. Observers rarely reported clockwise motion for the stimulus without motion lines, but often reported clockwise motion for the stimulus with motion lines. We interpret the data as evidence that motion lines bias observers' percepts of moving stimuli. Motion lines can contribute to percepts of motion.
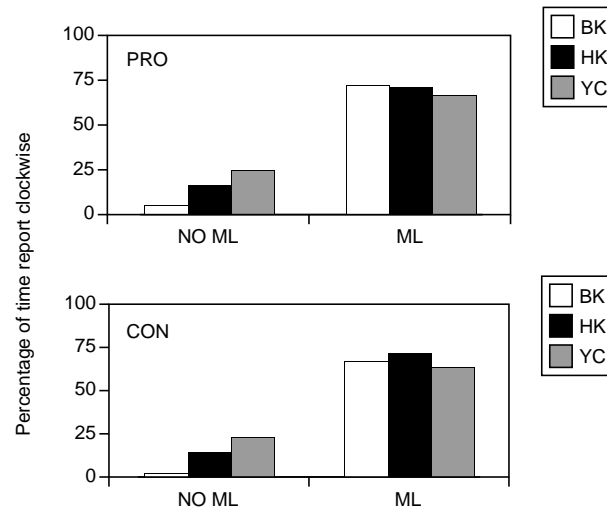
Figure 8: Asking observers to try to force the dots to move clockwise (PRO) or not clockwise (CON) has no effect on the frequency of observing clockwise motion. This suggests that the influence of motion lines is not due to cognitive factors that could bias ambiguous percepts.

Exactly how motion lines contribute to motion percepts is not resolved by the previous finding. For example, the neural network model described here suggests that motion lines act as cues to motion and the visual system, in responding to those cues, is biased toward a particular interpretation of an otherwise ambiguous motion display. An alternative account is that the motion lines are processed as metaphors for motion direction and through attentional processes the observer forces the ambiguous motion signals to group in particular ways. It is indeed true that with sufficient practice one can "mentally" bias the perceived type of motion to be vertical or horizontal. With a bit more effort it is also possible to force the percept to be of clockwise motion.

Thus, the experimental data support the idea that motion lines influence percepts of ambiguous motion displays, but it is not clear whether the mechanisms underlying such influence are perceptual or attentional. To try to disentangle perceptual and attentional effects, we asked subjects to participate in two more sessions of the experiment. The methods and procedures were exactly the same as before, except observers where asked to try to force the dots to move in a particular manner. In the second session observers were asked to try to make the dots move clockwise. In the third session observers were asked to try to make the dots not move clockwise. We refer to these sessions as PRO and CON, respectively.

We reasoned that if motion lines simply resulted in increased attentional biases for clockwise motion, then having observers mentally apply such attentional biases should cause the differences between the no-motion line and motion line conditions to disappear. If a difference remains, then it is more plausible that the effect of motion lines is not exclusively the result of attentional biases. Such a result would lend credence to the perceptual account we have offered. Likewise, if observers actively try to not see clockwise motion, but there still remains a significant percept of such motion for the motion line display, this is evidence that motion lines directly contribute to motion percepts.

Figure 8 plots the data for the two sessions. The results are essentially the same as in Figure 7, with attentional bias hardly effecting the percentages of reported clockwise percepts. These findings suggest that attentional biases are not responsible for the increased frequency of perceiving clockwise motion for the motion line display.

In a less formal study, we have changed the design of the motion lines so that they indicate counterclockwise, vertical, or horizontal motion. The results are essentially unchanged, with high frequency of seeing

the motion direction implied by the motion lines. As a whole then, the experimental data demonstrate that motion lines do contribute to motion percepts and are not limited to implied motion in static images. Moreover, the effects of motion lines on the ambiguous display suggest that they are not simply working through attentional biases, as a metaphorical explanation of motion lines would imply. The results are consistent with the proposed hypothesis that motion lines are one of many cues to motion generated by real moving objects, and that the visual system is tuned to detect the motion line cue.

5 Conclusions

By analyzing the behavior of a neural network in response to moving stimuli, we have shown that the model provides a computational and perceptual explanation of motion lines. Since the model has already accounted for a wide variety of psychophysical and neural data on motion, brightness, texture segmentation, figure-ground separation, and dynamic vision, the new account of motion lines links aspects of picture perception to a large literature of visual perception in general.

Although we suggest that motion lines have a computational and perceptual basis, this does not preclude influences from metaphorical interpretations of images. Kennedy (1982) convincingly argues for a metaphorical interpretation of many aspects of picture perception, and we suspect they play a role in motion lines as well. However, both computational and experimental analyses suggest that there is a strong perceptual component that guides the interpretation of motion lines in static images as cues to motion.

We anticipate that an analysis of motion lines and neural mechanisms tuned to detect motion lines as cues to motion will improve our understanding of motion perception in general. For example, McBeath, Shaffer and Kaiser (1995) noted in a discussion of object tracking that stimuli do not leave observable trajectories behind them as they move. In contrast, our analysis of the neural network model suggests that a moving object can, under the proper circumstances, leave a trail of signals that provide information about the object's trajectory. The trajectory trail could be processed by the spatial analyzing parts of the visual system to predict future paths of the object. The link between spatial and motion aspects of visual perception would tie together areas of perception that have previously been considered distinct.

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Appendix

In the simulations, a 4×6 pixel bar on a 20×14 image plane was filtered by oriented detectors that fed into a gated dipole circuit. The orientation detectors were identical to Levels 1–4 in Grossberg and Todorović (1988) and are not described here. The output of Level 4, Y_{ijk}, codes the response of an oriented cell at position (i, j) in the pixel plane that is tuned to orientation k. For our simulations we used only two cell orientations: horizontal, $k = 0$, and vertical, $k = 1$. The Y_{ijk} values were recalculated for every change in the position of the moving bar stimulus.

At each pixel location, these values fed into a gated dipole competition across orientation. Each cell in the gated dipole (see Figure 2), at each pixel position, obeyed a differential equation. The activity of the first cell obeyed the equation:

$$\frac{dV_{ijk}}{dt} = -V_{ijk} + Y_{ijk} + A, \tag{1}$$

where $-V_{ijk}$ indicates passive decay and A indicates a constant source of input to each pathway. Activity then passed through a habituating gate that obeyed a differential equation of the form:

$$\frac{dT_{ijk}}{dt} = B \left(C - T_{ijk} - T_{ijk} V_{ijk} \right). \tag{2}$$

The term $C - T_{ijk}$ indicates a production process whereby the amount of transmitter grows toward the value C. The term $-T_{ijk}V_{ijk}$ models how transfer of information to the next level uses a proportion of available transmitter. The entire equation was multiplied by $B << 1$, to indicate that the dynamics of the transmitter was much slower than the dynamics of neural activities.

The next level received the gated flow of activation. Cells at this level obeyed equations of the form

$$\frac{dW_{ijk}}{dt} = -W_{ijk} + T_{ijk}V_{ijk}. \tag{3}$$

The final level received excitatory input from the same pathway and inhibitory input from the orthogonal pathway. Thus, a horizontal cell obeyed an equation of the form

$$\frac{dZ_{ij0}}{dt} = -Z_{ij0} + W_{ij0} - W_{ij1}. \tag{4}$$

Each Z_{ijk} was compared to a threshold of 0.1 and any values above the threshold were used to produce Figures 3, 4 and 5.

In all simulations $A = 1$, $B = 0.001$ and $C = 1$. All equations were integrated using Euler's method with a step size of 0.0001. The (arbitrarily coded) intensity of the bar was 9 on a background of 4.5.