



Perceived motion in orientational afterimages: direction and speed

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Abstract

Two sets of experiments demonstrate new properties of motion in orientational after-effects. In a previous report, we showed that when observers adapted to a static bar grating whose elements varied in size or intensity from one side to the other, offset of the grating resulted in a motion after-effect, with the perceived motion in the direction of the largest or most intense bar. In the first new experiment, we show that similar results can be produced by varying the duration of the bar elements, with the direction of the motion after-effect toward the bar with the longest duration. In the second new experiment we demonstrate that the perceived speed of the motion aftereffect is influenced by the spatial extent of the after-effect, with larger extents corresponding to faster speeds. The experimental findings are discussed in the context of a neural network theory of visual perception. In this theory, a moving oriented contour leaves a trail of activity among cortical cells tuned to orthogonal orientations. We hypothesize that the grating stimuli produce after-effects that mimic the pattern of oriented responses produced by a true moving contour, and the visual system interprets this pattern as a cue for motion. We also show how the model connects the properties of these motion after-effects to properties of visual persistence. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Adaptation to a bar grating produces an after-effect consisting of shimmering lines that are oriented orthogonal to the original grating (Purkinje, 1823 [cited in Wade, 1996]; Pierce, 1900; Hunter, 1915; MacKay, 1957). These orientationally based afterimages are sometimes called complementary after-images (CAIs) to indicate that the shape of the after-image is, in some sense, the orthogonal complement of the inducing image. The lines of the CAI also seem to move in a direction orthogonal to the orientation of the inducing grating elements. For a vertically oriented bar grating with equal size and intensity elements, the CAI shimmers seem to move horizontally, with left or right directions possible (MacKay, 1961).

Recent findings in Kim and Francis (2000) demonstrate that the direction of CAI movement can be

controlled by introducing inhomogeneity in the inducing image. In the case of an oriented bar grating, Kim and Francis showed that gradual changes in bar intensity or bar size from one side to the other produced a CAI with motion in the direction of the most intense or largest bar.

These properties of CAI motion were predicted by analysis of a neural network theory of visual perception called the Boundary Contour System, or BCS, (Grossberg & Mingolla, 1985a,b). To enhance its processing of static images, this model uses strong excitatory feedback. However, analysis of this feedback for dynamic images revealed that it could lead to very long persistence of neural activity, which would correspond to unwelcome persistence of visual percepts and smearing of moving objects (Grossberg, 1991; Francis, et al., 1994). To curtail the undesirable persistence resulting from this feedback, Francis et al. (1994) proposed that when an image contour disappears, it generates a reset signal by causing a brief rebound of activity in cells tuned to the orthogonal orientation of the original contour. This rebound inhibits the neural circuits responsible for the excitatory feedback and curtails per-

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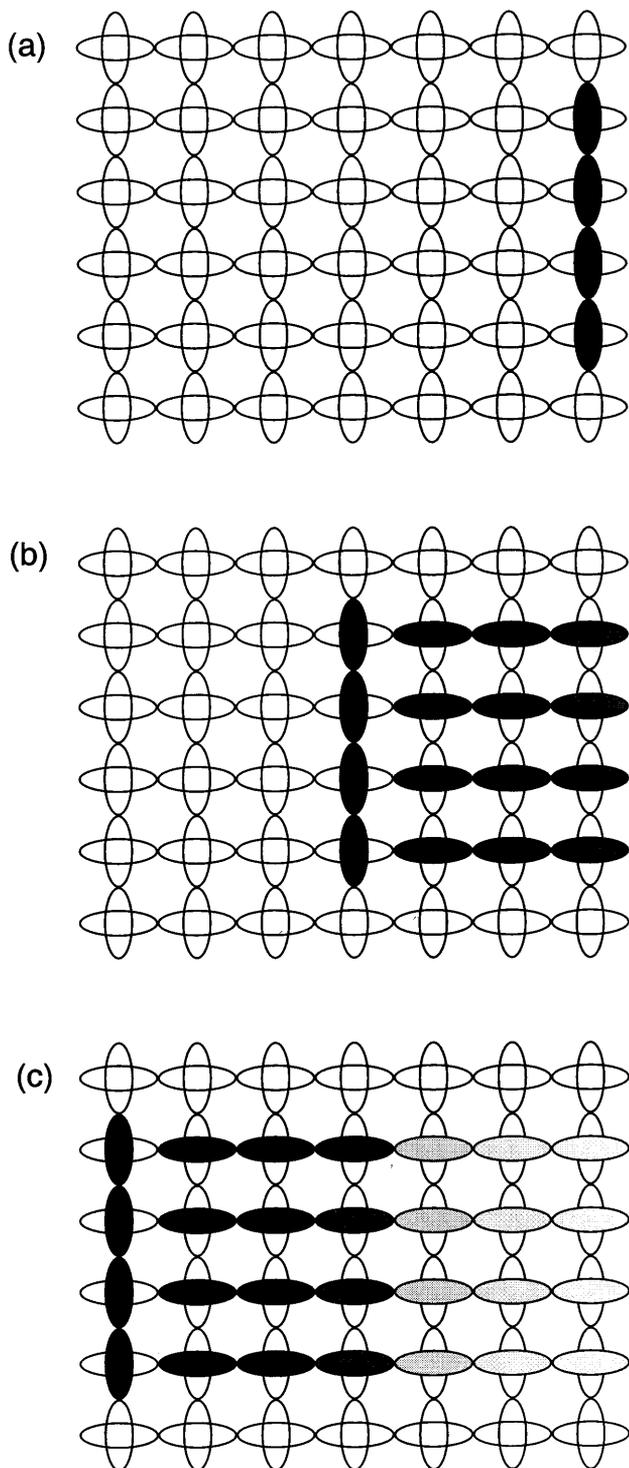


Fig. 1. Hypothesized behavior of orientationally tuned cortical cells in response to a moving vertical bar. (a) At the start of the movement, the bar excites a column of vertically tuned cells. (b) As the bar moves, disinhibited rebounds of activity generate a trail of horizontal activities. (c) As the bar moves further, the beginning parts of the trail grow weaker, thus creating a gradient of activities along horizontally tuned cells. We hypothesize that the visual system is tuned to the properties of this trail to identify stimulus motion, direction, and speed.

sistence. Computer simulations of the model demonstrated that it could account for psychophysical properties of visual persistence (Francis et al., 1994; Francis, 1999). Most notably, the model explains why persistence duration is inversely related to stimulus intensity, duration, and size. Increases in each of these stimulus characteristics lead to stronger reset signals at stimulus offset, and the stronger reset signals lead to shorter persistence duration. Coming back to CAIs, Francis and Grossberg (1996) suggested that the reset signals could account for CAI shapes because the reset signals corresponded to rebound responses among cells tuned orthogonally to the contours of the original image. Thus, the model predicts a close relationship between properties of visual persistence and CAIs. The model circuit responsible for the generation of reset signals is described in more detail in the conclusion.

Given the properties of the BCS model, Kim and Francis (1998) explored the pattern of orientational reset signals that would be generated by a moving stimulus. Consider a vertical bar moving from right to left in the visual field. In the model, such a bar produces disinhibited rebounds of activity among horizontally tuned cells along its movement path, as schematized in Fig. 1. Such a trail of orientational rebounds contains information about the bar's movement. For example, the relative strengths of responses within a trail provide information about the direction of motion. The strongest horizontal responses will be closest to the stimulus, with weaker responses near where the bar started moving (Fig. 1c). Likewise, the speed of a moving bar is partly coded by the length of its rebound trail, with faster stimuli leaving longer trails. These properties were simulated by Kim and Francis (1998) and they proposed that the visual system is sensitive to the properties of rebound trails as indicators of motion direction and speed. In particular, responses of horizontally tuned cells along a horizontal line should be a cue that something has moved horizontally. The gradient of response strength along the line indicates the direction of the movement, and the length of the line gives a relative indication of the movement speed.

Kim and Francis (2000) suggested that CAIs include a motion after-effect because they produce a pattern of responses among orientationally tuned cells that is similar to the pattern produced by a rebound trail when a stimulus actually moves. Furthermore, they showed that by introducing an intensity or size gradient among a grating's bars, the CAI motion was in a direction toward the most intense or largest bar. This was predicted by the model on the basis of known properties of visual persistence. A gradient of intensity or size among the bars leads to a gradient of reset signal responses at grating offset. This pattern of reset signals should closely resemble the pattern produced by a moving stimulus (as in Fig. 1c).

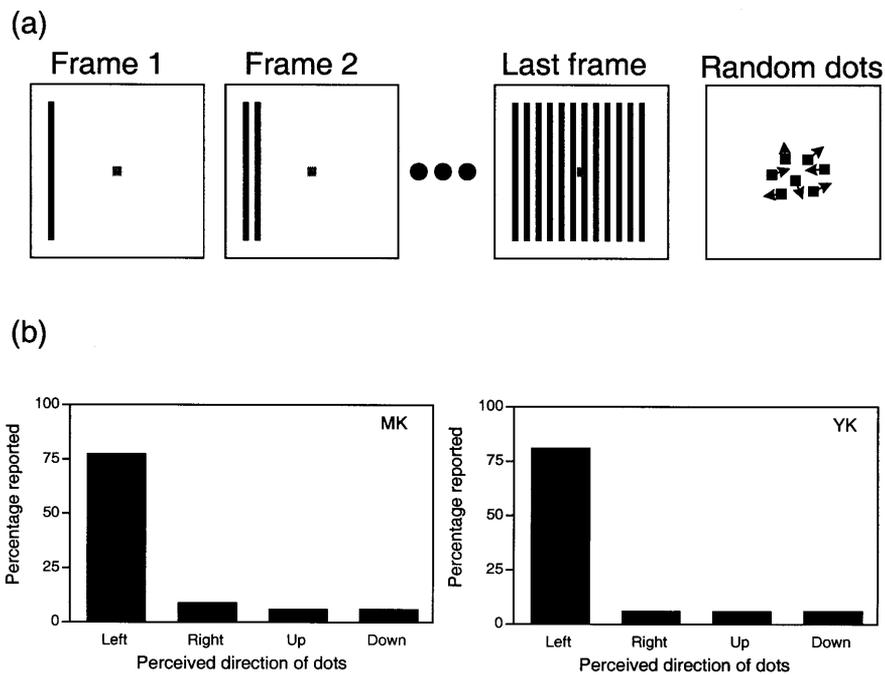


Fig. 2. Experiment 1. (a) A schematic of the sequence of images. A bar grating was gradually built from left to right, and then the grating's offset was followed by randomly moving dots. The observer's task was to judge the perceived direction of movement of the dots. (b) Percentages of observed motion directions among the random dots for two observers (MK and YK). There was a high percentage of leftward motion reported.

We now report two additional experiments that further support the model's explanation of CAI motion. The first experiment is a direct test of the model's hypothesized connection between properties of visual persistence and CAI motion. We show that a CAI inducing stimulus with a gradient of durations among grating bars produces CAI motion toward the bar with the longest duration. A second set of experiments verifies that the rebound trail is used not only as a cue for motion direction, but also for motion speed. In combination with the results in Kim and Francis (2000) these results provide strong evidence for the theory's explanation of CAI motion and provide external validity of many aspects of the theory's mechanisms.

2. Experiment 1: CAI direction and stimulus duration

As in the experiments of Kim and Francis (2000), the goal of this experiment was to create an inducing stimulus that would produce a CAI pattern of responses among orientationally tuned cells that mimics the rebound responses created by a moving stimulus. If the visual system is sensitive to this pattern as a cue to motion, then the CAI should include a corresponding motion percept.

Based on our previous studies (Kim & Francis, 2000) the model hypothesizes that any stimulus characteristic that influences the strength of reset signals will also be capable of controlling the direction of CAI motion.

This connection was already shown for stimulus intensity and size. Studies of visual persistence also report an inverse-duration effect (Bowen, et al., 1974), where stimuli presented for longer durations have shorter persistence. Francis et al. (1994) hypothesized that this was due to stimuli with longer durations producing stronger reset signals, which resulted in shorter persistence. If this explanation of the inverse-duration effect is correct, then varying the duration of bars in a grating should produce a gradient of reset signal strengths at offset of the whole grating. This gradient of reset signal strengths should mimic a rebound trail produced by a moving stimulus, so the CAI for such a stimulus should include motion in the direction of the bar with the longest duration. Failure to find an influence of bar duration on CAI motion would constitute a significant challenge to our explanation of CAI motion. Experiment 1 tests this model prediction.

2.1. Method

Fig. 2a schematizes the presentation of the inducing grating. The observer focused on a small fixation point in the center of a computer screen. A bar grating was then drawn by adding one bar at a time, from left to right. There was a lag of 1.2 s between the addition of each bar. After the full grating was presented for 1.2 s, the entire grating turned off. Seven hundred milliseconds after grating offset, randomly moving dots were presented for 210 ms. Pilot studies indicated that the

CAI motion captured the perceived motion of the random dots. The observer's task was to indicate the perceived dominant direction of movement among the dots.

All stimuli were presented on a Silicon Graphics Indy computer. The full grating consisted of 25 black (0.06 cd/m^2) bars on a white (52 cd/m^2) background. Each black and white stripe of the grating had a thickness of 28 min and a height of 25 degrees. The subsequently presented 200 random dots were restricted to a 13 by 13 degree square filling the center of the monitor. Each dot was a small square subtending 7 min on each side, and was gray (41 cd/m^2) on white. A dot changed position from one frame to the next, moving 15 min in a vertical and/or horizontal direction, with frame duration being approximately 30 ms. During a testing session, an observer made 32 judgments on the perceived direction of the random dots and eight judgments for each of four directed movement conditions (described below). The different dot conditions were randomly mixed during a session. A testing session lasted approximately 1 h.

Two observers, naive to the purpose of the study and with normal or corrected-to-normal vision, each participated in one testing session.

2.2. Procedure

In half of the trials all dots moved in random directions from one frame to the next. A new random direction was chosen for each dot and each pair of frames. The other trials were catch trials, where 25% of the dots (different dots for each pair of successive frames) moved in a fixed common direction along one of the major axes, while 75% of the dots moved randomly. The observer's task was to report the strongest perceived direction of movement among the presented dots. The choices were restricted to up, down, left, or right, and observers were asked to make their best judgment if none of these choices were clearly applicable. After making a choice with a keypress, an observer started the next trial with another keypress.

2.3. Results

Fig. 2b plots the percentages of reported directions on the random dot direction trials. The data are nearly identical for the two observers; and both show a strong tendency to report leftward motion of the dots. This motion is toward the longest duration bar, as predicted by the model. On the catch trials, observers tended to report motion consistent with the non-random movement of dots (82 and 84% of trials for MK and YK, respectively).

This finding validates the hypothesized connection between properties of visual persistence and CAI mo-

tion. Stimulus variables that influence visual persistence (intensity, size, and duration) can also control motion direction in CAIs. These results strongly support the BCS model's explanation of both visual persistence and CAI motion.

2.4. Control

We ran an additional experiment to exclude an alternative hypothesis for the results of experiment 1. The sequential presentation of the bars produced rightward motion, and it is conceivable that the observed leftward motion after-effect was thus a standard motion after-effect and not dependent on the presence of the CAI. Given the long durations of individual frames (1.2 s), we would be surprised if this account would hold up, but we tested it with a variation of experiment 1. We repeated experiment 1, but now each frame showed only the most recent bar of the grating and not the previously drawn bars. The sequence of bars is schematized in Fig. 3a. A single bar stepped from left to right 25 times in 1.2 s intervals. This sequence of bars produced the same type of motion (if any) that was produced by the sequential appearance of bars in experiment 1. If the motion after-effect in experiment 1 is due to motion from the sequential presentation of elements, we would expect that offset of the stepping bar would lead to reports of leftward motion as in experiment 1. However, if the perceived motion in experiment 1 is based primarily on a CAI trail, we would expect that a single bar jumping across the screen from left to right would not produce a strong leftward motion after-effect.

Two new observers participated in this experiment, one was an author and the other was naive to the purpose of the study. Each observer had normal or corrected-to-normal vision and participated in one experimental session. The stimuli and procedures in the second experiment were the same as in the first, except that the presentation of the bars was as schematized in Fig. 3a.

On the catch trials, observers reported that the general direction of movement was the same as the direction of the non-randomly moving dots on 75 and 78% of the trials for YSC and GF, respectively. Fig. 3b plots the percentages of reported directions on the random dot direction trials. There were differences between observers, with YSC reporting predominately upward motion on the random dot trials, while GF tended to report rightward motion most often. Both observers rarely reported downward motion. Neither observer tended to report leftward motion at an elevated percentage. The data do not support the hypothesis that motion of the bar produces a standard motion after-effect in the opposite direction.

The variability between subjects in the control experiment is quite different from experiment 1, where the CAI motion seemed to dominate the percept. This variability is consistent with the view that subject biases, rather than a CAI after-effect, are influencing the perceived direction of the randomly moving dots in the control experiment. If such biases exist in experiment 1, they are being swamped by the larger effects of CAI motion.

3. Experiment 2: CAI speed

In their simulations, Kim and Francis (1998) noted that faster moving stimuli leave a longer trail of oriented rebounds. They hypothesized that the length of the trail could be used as a cue for relative movement speed. If this hypothesis is true and if the visual system's interpretation of rebound trails is the basis for perceived motion in CAIs, then it should be possible to manipulate the perceived speed of the CAI by influencing the spatial extent of the CAI pattern. Fig. 4 schematizes how CAI spatial extent should be related to perceived speed. Fig. 4a and b schematize the oriented rebounds among horizontally tuned cells that should be created in response to fast and slow movement of a vertical bar, respectively. The fast movement should leave a longer trail of horizontal responses because it reaches the far left side before the responses on the far

right have faded.

Although the model predicts that properties of the rebound trail contain information about the relative speed of movement, it is not a necessary prediction that the visual system uses this information. It is easily conceivable that the visual system uses the direction-specific information in rebound trails as in experiment 1 and Kim and Francis (2000), but ignores the speed-specific information. Nevertheless, if the visual system does use the speed information in rebound trails, then the model predicts properties of the trail that should influence perceived speed of motion in CAIs.

Fig. 4c, d, and e schematize the pattern of oriented responses produced by offset of various inducing gratings. All of these gratings have varying sizes of bars that increase from right to left, so the strongest oriented rebound would be on the left (Francis, 1999). Kim and Francis (2000) showed that the resulting CAI has motion in the direction of the larger bars (leftward). By varying the size (Fig. 4c versus d) or contrast (Fig. 4c versus e) of the inducing grating, the theory predicts that the resulting CAIs will have a faster speed for the larger CAI. For the low contrast grating in Fig. 4e, we suppose that the bars on the far right produce oriented rebounds below threshold because they are both low contrast and thin, and thereby produce the weakest reset signals. The theory predicts that the CAI from viewing Fig. 4c will be faster than the CAI from viewing the grating in either Fig. 4d or e.

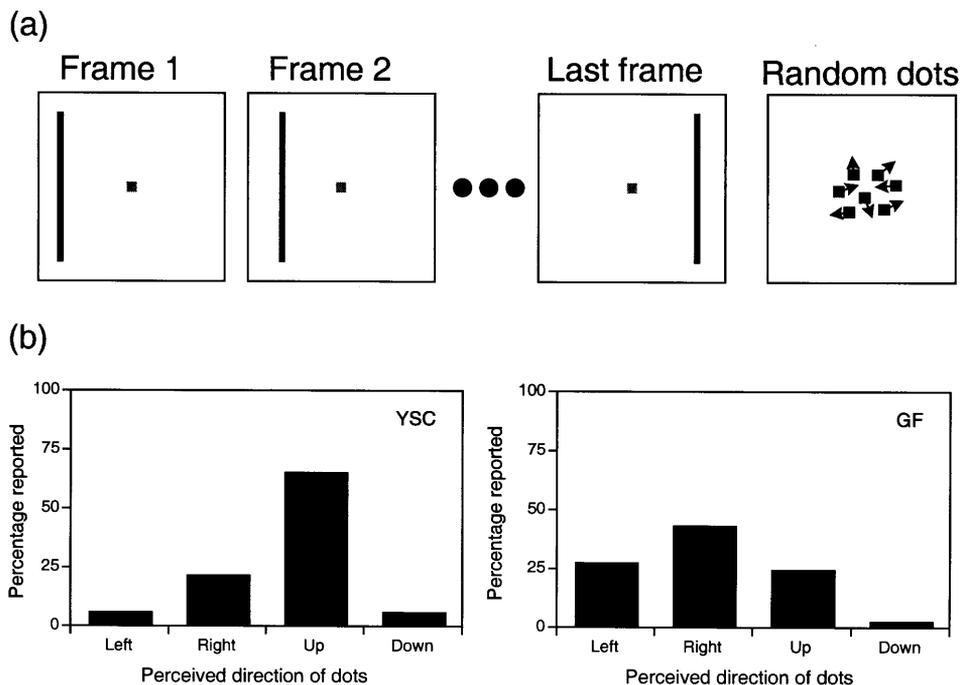


Fig. 3. Control for experiment 1. (a) A schematic of the sequence of images. The individual bars of a grating were presented sequentially from left to right, and then the grating's offset was followed by randomly moving dots. The observer's task was to judge the perceived direction of movement of the dots. (b) Percentages of observed motion directions among the random dots for two observers (YSC and GF). Leftward motion was not often reported.

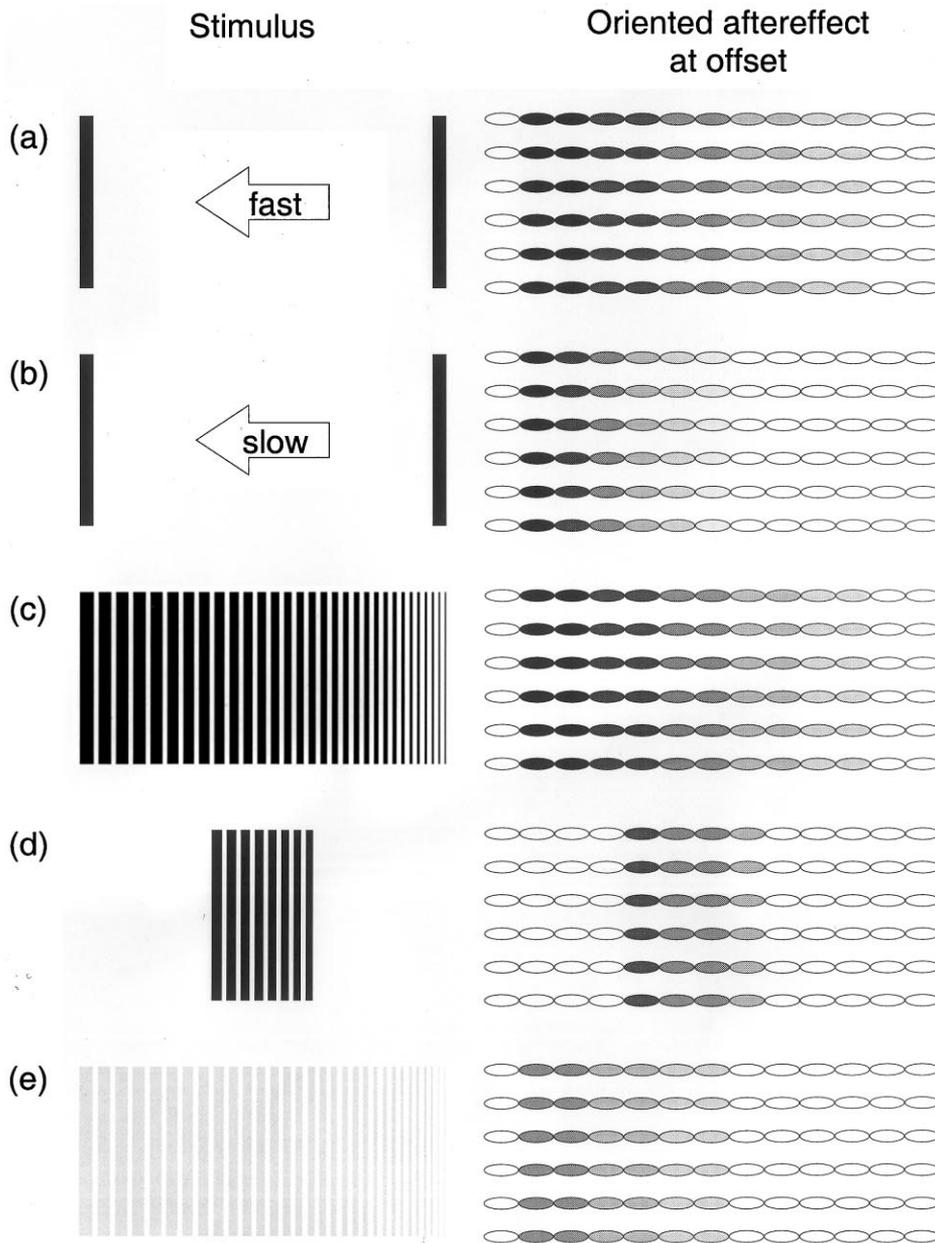


Fig. 4. Schematic of the hypothesized oriented after-effect for different types of stimuli. The ellipses on the right indicate cells in the visual cortex that code horizontal orientations. Darker shades of gray code stronger responses among these cells. (a) Fast movement of a vertical bar from right to left produces a long trail of CAI responses among the horizontal cells. (b) The trail produced by a bar moving more slowly produces a shorter trail because the CAI has already faded at the far right. (c) A large grating produces a CAI similar to in (a), thereby implying fast movement. (d) A smaller grating produces a shorter CAI, which implies slower movement, as in (b). (e) A low contrast grating produces a weaker CAI which is also shorter than in (c) because the CAI on the far right is below threshold. This CAI is consistent with slow movement as in (b).

3.1. Methods and procedures

The experiments were similar to those above, except two gratings and two random dot patterns were presented simultaneously and the observer judged which set of random dots seemed to move faster. Fig. 5a schematizes the sequence of displays during one type of experimental trial. An observer fixated on a small spot in the center of the screen. Two gratings were presented

above and below this fixation spot. For the experiment schematized in Fig. 5a, the smaller grating is a subset of the middle bars of the larger grating. After 30 s of adaptation, the bar gratings were turned off and 700 ms later a pair of random dot motion patches were presented in the locations of the grating centers. The random dot movements lasted for 240 ms. Each random dot patch consisted of 100 random dots restricted to a 7.7 degree square. The observer's task was to

report which patch of dots seemed to have faster movement.

Fig. 6a schematizes a different type of comparison where the gratings are equal in length, but differ in contrast relative to the background. The high and low contrast inducing gratings were rectangular-shaped, with edges filling a width of 28.7 degrees and a height of 14.4 degrees. The edge-to-edge distance between gratings was 2.0 degrees. For the high contrast grating, the 31 bars were all black (0.06 cd/m^2) on a white background (52 cd/m^2). For the low contrast grating, all bars were gray (40 cd/m^2). The largest bar had a thickness of 65 min, the thinnest bar had a thickness of 3 min, and intermediate bars had thicknesses linearly related to the extremes. The white space between two adjacent bars was held constant at 28 min. The smaller sized grating, schematized in Fig. 5a, consisted of eight black bars, with the largest bar having a thickness of 46 min, and the smallest bar a thickness of 29 min. The

larger inducer grating had the same sized bars at the corresponding places in the display. In a pilot study we insured that all of these gratings produced a noticeable CAI upon their offset.

To prevent bias effects, the duration of the frames in a random dot patch was varied. On a quarter of the trials each patch had frame durations of approximately 30 ms (fast movement), whereas on another quarter of the trials each patch had frame durations of approximately 60 ms (slow movement). The other half of the trials were catch trials, with one patch fast and the other slow. The faster dot patch was assigned to the top or bottom an equal number of trials. Each observer participated in four testing sessions, with locations (top/bottom) of the large/small or high contrast/low contrast inducing images fixed for an entire session. Each session consisted of 16 trials for every combination of dot patch speeds, for a total of 64 trials in a session. Two observers, naive to the purpose of the

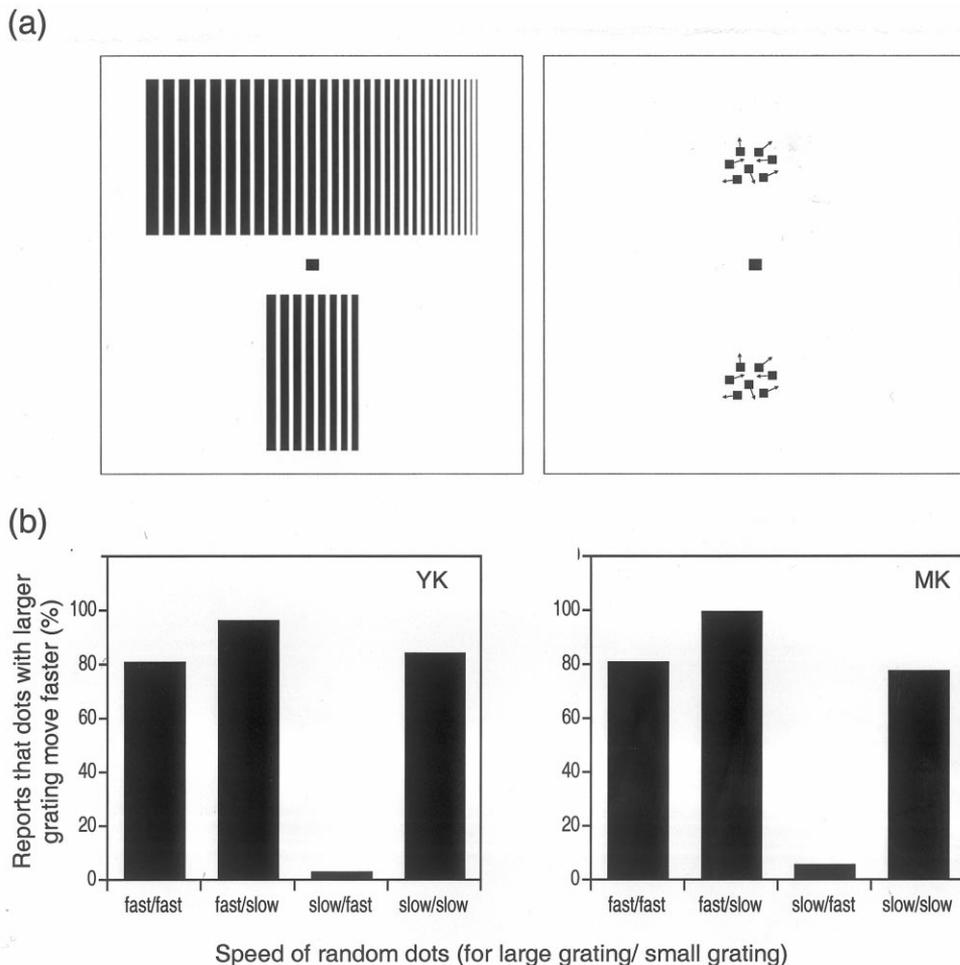


Fig. 5. Experiment 2, comparison of spatial extent. (a) A schematic of the sequence of images. Observers fixated the small central square and then viewed a pair of random dot patches. The observer's task was to judge whether the top or bottom patch seemed to contain faster movement. (b) Percentage of trials in which an observer reported faster movement for the patch associated with the larger grating for two observers (YK and MK). When the two patches had the same physical speed (fast/fast and slow/slow) each observer tended to report that the patch associated with the larger grating seemed to move faster.

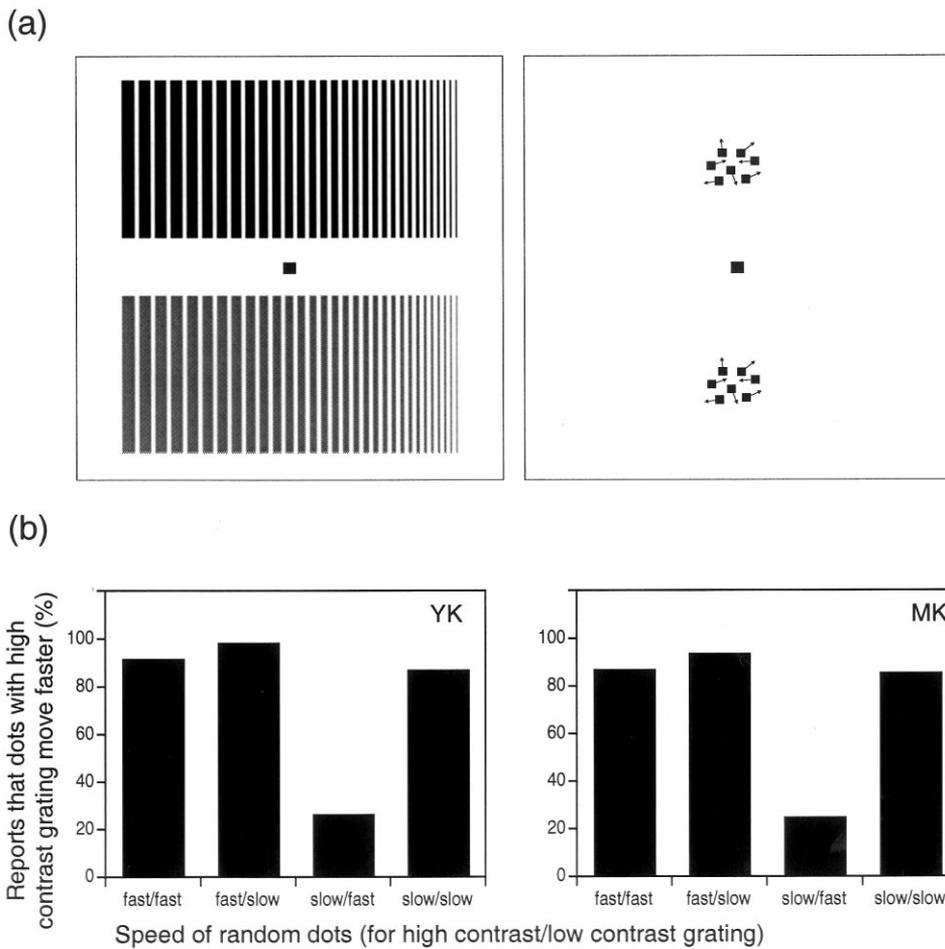


Fig. 6. Experiment 2, comparison of grating contrast. (a) A schematic of the sequence of images. Observers fixated the small central square and then viewed a pair of random dot patches. The observer's task was to judge whether the top or bottom patch seemed to contain faster movement. (b) Percentage of trials in which an observer reported faster movement for the patch associated with the higher contrast grating [top in (a)] for two observers (YK and MK). When the two patches had the same physical speed (fast/fast and slow/slow) each observer tended to report that the patch associated with the higher contrast grating seemed to move faster.

study and with normal or corrected-to-normal vision, participated.

3.2. Results

In analyzing the results there were no significant differences between the top or bottom placement of the inducing gratings, so the data were averaged across those conditions. Fig. 5b plots the percentage of trials in which an observer reported that the dots associated with the larger grating seemed to move faster than the dots associated with the smaller grating. Each percentage is based on 32 trials. On the catch trials (fast/slow and slow/fast) observers usually correctly identified which patch had the faster movement regardless of inducer type. On the test trials (fast/fast and slow/slow), observers often reported that the dots associated with the larger grating seemed to move faster than the dots associated with the smaller grating.

Similar results are shown in Fig. 6b for the comparison of high and low contrast gratings. On the catch trial conditions, slow/fast and fast/slow, observers often correctly identified which dots were moving faster. On the test trials (fast/fast and slow/slow), where the dots had the same frame durations, observers reported that the dots associated with the high contrast grating seemed to move faster. There is a tendency for dots associated with the higher-contrast grating to be perceived as moving faster, even when they are physically moving slower (condition slow/fast). This suggests that the CAI speed motion effect, that makes the dots associated with the high contrast grating seem to move faster, can sometimes overcome a physical speed difference.

Overall, this is clear evidence in support of the prediction that a larger spatial extent of a CAI corresponds to faster movement. Moreover, because there is no actual movement in the inducing stimulus, it is strong support for the hypothesized connection between trails of oriented rebounds and perceived motion.

3.3. Control

We also ran a control experiment to rule out a possible alternative explanation. One could argue that the larger, higher contrast, grating produces a stronger CAI and so is better able to produce a percept of coherent motion among the subsequently presented dots. If perceived speed was directly related to perceived coherency, that might account for the effect of CAI size on perceived CAI speed. To rule out this possibility we had two observers compare simultaneous dot patches with different percentages of dots that coherently moved to the left and judge in which patch the dots seemed to move faster. The experimental design was the same as for the CAI speed experiment, except there was no adapting stimulus, and the percentage of coherent movement among the dots was varied. The results are reported in Fig. 7, which plots the percentage of trials in which observers reported that the dots in the top display seemed to move faster than the dots in the bottom display. The separate curves are for trials with different coherency percentages in the top display. The *x*-axis is the coherency percentage of dots in the bottom display. The main effect is shown in two ways. First, every curve is generally increasing, which means that the higher the coherency of the dot movement in the bottom display, the more likely observers were to judge the top display as moving faster. Likewise, as coherency increases in the top display, the corresponding curve is lower on the graph, meaning the observer was less likely to report that the dots in the top display seemed to move faster. These effects can also be summarized by noting that when comparing two patches with different coherencies, the observers reported that the patch with the lower coherency seemed to move faster on 82% of the trials.

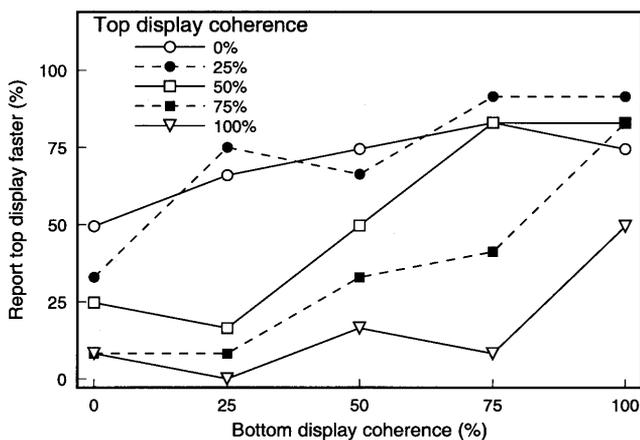


Fig. 7. Experiment 2, control. The percentage of trials that observers reported that a dot motion patch above the fixation point seemed to contain faster movement than a dot motion patch below the fixation point. There is an inverse relationship between the coherency of motion in the patches and the frequency of it seeming to contain faster movement.

Thus, the patch with more coherent motion seemed to move slower, which means coherency effects cannot account for the relationship between CAI size and perceived speed. The experimental findings on CAI speed seem to only make sense if the spatial extent of the CAI is related to perceived motion speed. And that connection makes sense only if a pattern of oriented after-responses is a cue to motion. No other current theory of motion perception can explain these results because those theories are built to only indicate motion when there are appropriate spatio-temporal changes in luminance or texture.

4. Conclusions

There are two strong conclusions to draw from the experimental data. First, we have offered additional evidence that there is a close relationship between the way the visual system responds to dynamic non-moving stimuli and the way it responds to moving stimuli. Namely, we suggest that a moving stimulus leaves a trail of neural responses among orientationally tuned cortical cells. A non-moving stimulus can produce a similar pattern of neural responses and thereby engender perceived motion. The control of direction and speed of CAI motion is entirely consistent with this suggestion, and is unexplainable by any other current theory of motion perception.

Second, there is a close relationship between the properties of CAI motion direction and properties of visual persistence. The theoretical connection between these domains is the use of reset signals in the BCS neural network theory (Grossberg & Mingolla, 1985a,b; Francis et al., 1994). To create reset signals, Francis et al. (1994) embedded a gated dipole circuit (Grossberg, 1972) in the design of the BCS model. Fig. 8 schematizes a gated dipole circuit whose separate pathways code orthogonal edge orientations. These orientation pathways compete with each other as signals pass from lower to higher levels of the circuit. Feeding this competition are inputs gated by habituating transmitters. Along with signals from external stimuli, each input pathway receives a tonic source of activity, and all output signals are rectified. At the offset of stimulation, a gated dipole circuit generates a transient rebound of activity in the previously non-stimulated pathway. In the overall design of the BCS, this rebound activity acts as a reset signal to curtail persisting neural signals.

The time plot next to each cell or gate describes the dynamics of this circuit. The sharp increase and then decrease of the time plot at the lower right of Fig. 8 indicates that an external input stimulates the horizontal pathway. This input produces both a response and habituation in the horizontal channel. Thus, when the

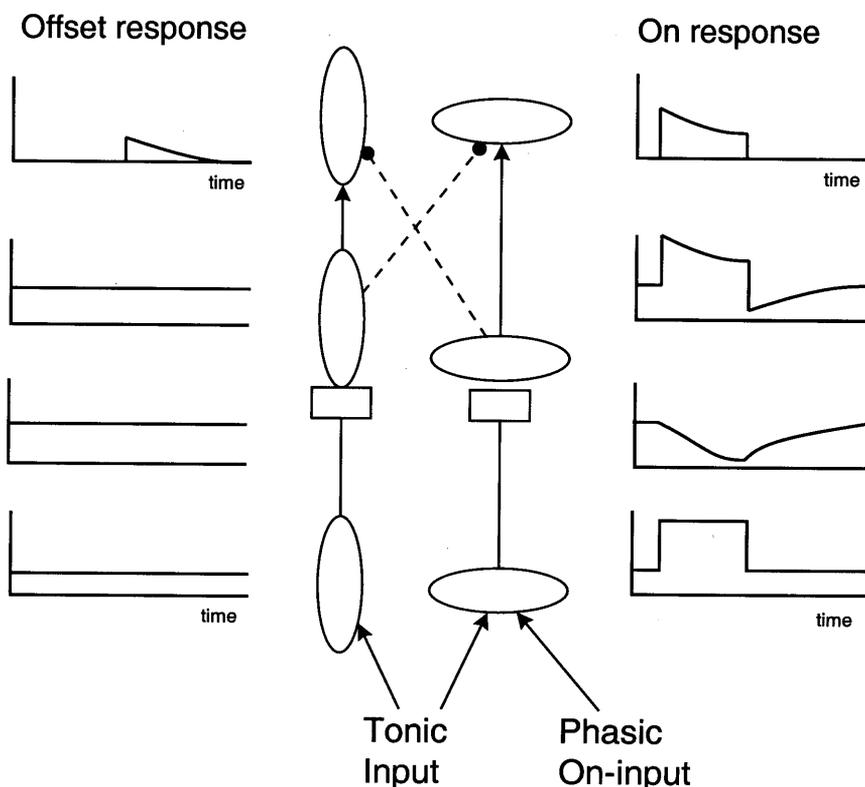


Fig. 8. At stimulus offset, a gated dipole circuit produces a transient rebound of activity in the non-stimulated opponent pathway. When the pathways code opposite orientations, offset of a horizontal input leads to a rebound of vertical activity. Dashed lines with circle terminators indicate inhibition, 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.

horizontal input turns off, the vertical channel wins the competition against the habituated horizontal channel to generate a rebound of activity. As the horizontal transmitter gate recovers from its habituated state, the rebound signal in the vertical channel weakens and finally disappears.

Francis et al. (1994) and Francis (1999) showed that the strength of the rebound signal generated by offset of a visual stimulus was directly related to the intensity, duration, and size of the stimulus. Moreover, the stronger the rebound signal, the shorter the duration of persisting neural responses to the visual stimulus. Through computer simulation, these properties explained the empirical findings of inverse-intensity, inverse-duration, and inverse-size effects for visual persistence (Bowen et al., 1974; Meyer & Maguire, 1977).

In the model, a bar grating that varies in intensity, duration, or size produces a gradient of rebound response strengths at offset. The findings of experiment 1 and Kim and Francis (2000) demonstrate that this gradient of rebounds is a cue to motion. This is a strong verification of both the idea that a trail of rebound signals is a cue to motion in a particular direction and the idea that a gated dipole circuit is

responsible for control of visual persistence and the existence of the rebound trail.

Our theory hypothesizes a connection between the spatial arrangement of responses among oriented cells that are produced by gated dipole responses to a moving stimulus. This is a change from typical theories of motion perception because it claims that some part of the visual system responds to a static representation of spatio-temporal changes (the rebound trail) and does not necessarily need the actual spatio-temporal changes to drive motion computations. While the data are entirely consistent with this hypothesized connection, it is important to rule out other possibilities. For example, the variations in intensity, size, and duration of bar elements will give rise to different persistence durations. For a variation in size, larger bars have shorter persistence durations. Thus, at physical offset of a bar grating whose elements increased in size from right-to-left, the disappearance of bars would be from thickest to thinnest. If perceived motion was based on the spatio-temporal disappearance of these bars, the motion signal would be from left to right. This is opposite to the direction found by Kim and Francis (2000), so offsets of persisting elements cannot explain CAI motion direction. Moreover, the effects of CAI

motion in our experiments are measured 700 ms after offset of the grating, which seems much too long to be explained by any direct properties of visual persistence.

What about the spatio-temporal properties of the gated dipole rebounds? Depending on the details of time scales in the gated dipole, it is likely that the order of appearance of each gated dipole rebound is directly related to the rebound's ultimate strength. Thus, offset of a bar grating whose elements increased in size from right-to-left, would lead to the appearance of gated dipole rebounds, whose elements appeared in order from left to right. The spatio-temporal ordering of these rebounds would suggest motion to the right, which is the opposite of what is observed experimentally. Thus, the spatio-temporal properties of the appearance of rebounds cannot explain CAI motion.

On the other hand, a stronger gated dipole rebound does last longer. A set of gated dipole rebounds that are strongest on the left and weakest on the right will disappear (drop below a threshold value) from right to left as the weaker rebounds fade away sooner. Thus, the spatio-temporal properties of the offset of rebounds does correctly predict the direction of CAI motion. However, we feel this explanation cannot adequately capture the perceived duration of CAI motion. The disappearance of rebound signals is a one-time event that cannot be repeated in the visual system. This would suggest that the motion percept should also be a one-time event that occurs over a short span of time. The percept of CAI motion, however, is of streaming continuous motion that lasts for several seconds. This property makes us believe that CAI motion is based on a static representation of movement rather than based on computations from spatio-temporal changes. The rebound trail is acting as a type of iconic memory for movement. As long as that representation is present, the visual system reports that motion is present.

Other theories of motion perception have been proposed that make similar claims about a trailing response that represents movement. However, they cannot account for our data because they fail to connect the important relationship between gated dipole based reset signals and the rebound trail. Shepard and Zare (1983) demonstrated that an apparent motion stimulus seemed to follow a path indicated by a brief faint arc flashed during the interstimulus interval. They hypothesized that the arc was interpreted by the visual system as motion blur. Geisler (1999) hypothesized that oriented cells in the visual cortex may respond to motion streaks and that these responses may code motion parallel to a cell's orientation (see also Harrington et al., 1980). However, these approaches will require modification if they are to account for our results. Shepard and Zare's hypothesis gives no explanation why a CAI would have a motion component as there is nothing that seems to be a motion blur. Geisler's model

detects the axis of motion on the basis of a single oriented cell's response to a motion streak. Such a model correctly predicts that oriented responses can indicate motion along an axis parallel to their orientation, but it cannot explain why, in our experiments, motion is seen primarily in one direction along the axis. A single oriented cell in Geisler's model cannot represent a gradient of responses across the motion streak. Our results suggest that producing a gradient of responses across a set of orientationally tuned cells is critical for controlling the direction of CAI motion. Geisler's model could be modified so that the interpretation of motion streaks occurs at a higher level of the visual system, as we have proposed. But without an appreciation of the reason that such an interpretation is necessary, this modification is ad hoc.

In contrast, our theory is justified and verified in every component. As Grossberg and Mingolla (1985a,b) demonstrated, excitatory feedback is necessary in neural circuits to adequately contain a filling-in process. Grossberg (1991) and Francis et al. (1994) showed that the excitatory feedback produces potential persistence problems unless gated dipoles are introduced to reset the feedback circuits. Francis and Grossberg (1996) showed that the gated dipole responses account for CAI shapes. Kim and Francis (1998) showed that the gated dipole circuits in the model leave a trail of responses that identify the direction, speed, and trajectory of a moving stimulus. Finally, Kim and Francis (2000) and the current results empirically verify the predicted properties of CAI motion on the basis of this theory. Moreover, there is neurophysiological support that offset of an oriented visual stimulus produces a response in cells tuned to the opposite orientation (Ringach et al., 1997), that the mechanisms of a gated dipole can exist at the cellular level (Abbot et al., 1997), and that some motion-sensitive cells in the visual cortex also respond to stimuli oriented parallel to the preferred direction of motion (Albright, 1984). Thus, there is strong computational, experimental, and neurophysiological data to support the model and its accompanying hypotheses.

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