

Levels of Motion Perception

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I shall present some new, or newish, illusions to show that motion signals in the early parts of the visual system are profoundly altered by stimulus luminance and contrast. I shall show that contrast affects (1) motion strength in time till breakdown; (2) motion strength in crossover motion; (3) speed in the footsteps illusion; (4) direction in the plaid-motion illusion; and (5) direction: split dots.

I shall then consider how it is that higher perceptual processes massage these neural motion signals into the perception of moving objects. For instance, moving line terminators help to solve the aperture problem. But these solutions are modified by stimulus contrast in the plaid-motion illusion and in the peripheral-oblique illusion. In the chopstick and sliding rings illusion, the motion of terminators propagates along straight lines and is blindly (and incorrectly) assigned to the motion of the central intersection.

Finally, a new display of moving dots alternates perceptually between two radically different perceptual interpretations. Usually the local percept (trees) is seen first, but the global interpretation (forest) gradually takes over in the course of time.

5.1 Introduction

In this chapter I shall review my own work, with my various co-workers, on levels of motion perception. I shall start with motion signals in the early parts of the visual system and show (with the aid of some newish illusions) how these are greatly affected by stimulus luminance and contrast. I shall then consider how it is that higher perceptual or cognitive processes manage to interpret these neural motion signals in order to achieve the real purpose, namely the perception of moving objects.

5.2 Illusory Rotation of a Spoked Wheel

Brian Rogers and I have studied apparent movement that occurs in a disk that is divided into sixteen stationary sectors of different grey levels. All the greys are stepped synchronously clockwise around the sectors, driven by color cycling

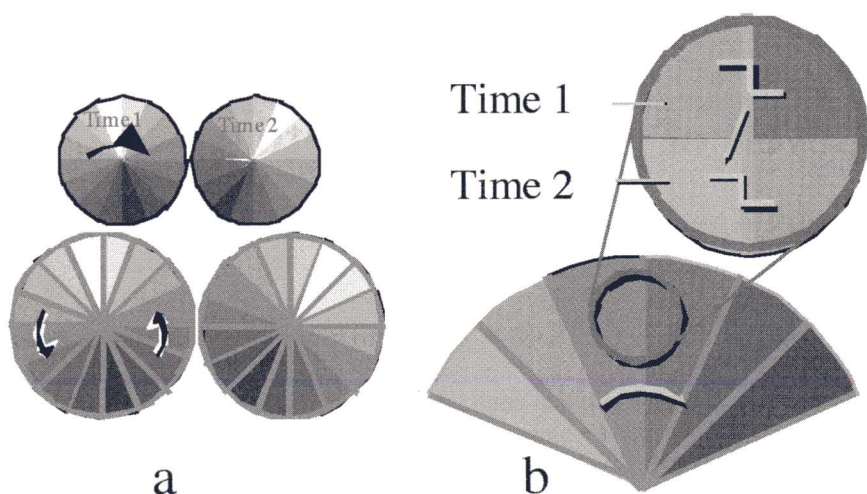


FIGURE 5.1. (a) A sectored disk jumps around clockwise (upper diagram). Superimposed stationary, unchanging grey spokes (lower diagram) appear to rotate counterclockwise. (b) Magnified view of a vertical spoke. A light/dark border at the right-hand edge of a spoke at time 1 jumps to the left-hand edge of the spoke at time 2. See text.

in the computer palette. The edges of the sectors never move; only the colors change. As a result, the sectors show continuous apparent clockwise motion. Figure 5.1 shows that the sectors rotate 45 deg clockwise between successive time frames. The interesting feature is the behaviour of the thin, stationary grey radial lines that lie along the edges of the sectors, looking rather like bicycle spokes. As the sectors appeared to rotate clockwise during the colour cycling, these radial lines appeared to rotate vigorously counterclockwise. When the color cycling was stopped after 20 seconds, all observers reported a strong clockwise motion aftereffect. This clockwise aftereffect cannot come from the sectors that had been jumping clockwise, but must come from the bicycle spokes that had been apparently moving counterclockwise. The presence of a motion aftereffect makes it likely that the "illusory" rotation of the spokes actually contains motion energy that stimulates neural motion detectors (Braddick, 1974; Adelson and Bergen, 1985). The spokes appeared to move only when they were thin (~ 5 min arc in foveal vision), and when their luminance matched the sectors they abutted.

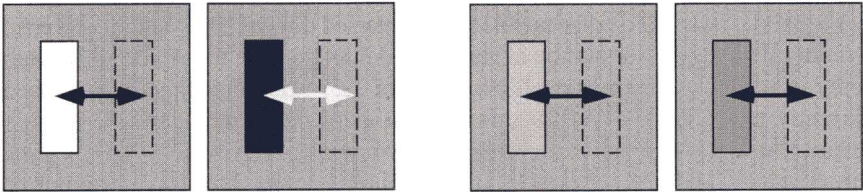
Various control experiments ruled out induced brightness and induced motion as explanations. Instead, Figure 5.1b shows our explanation. When the radial spoke straddles the luminance of two adjacent sectors, then as the sectors jump clockwise the right-hand edge of the spoke at time 1 jumps to the left at time 2, through the width of the spoke (only 5 min arc). Thus, as 16 sectors jump clockwise through a whole sector width, a spoke edge makes a tiny jump to the left. But this is sufficient to give the strong impression of motion, followed after inspection by a motion aftereffect from the spokes. We conclude that in motion, less is more. There must be many neural motion detectors with tiny receptive fields (or sub-

fields: see Barlow and Levick, 1965), in the order of 5 min arc in width. Motion detectors wide enough to respond to the huge jumps made by the sectors must be far less numerous or less sensitive. In conclusion, the apparent motion that we observed in our spoked wheel illusion results from actual small displacements of luminance contours in the reversed direction. However, our phenomenon does reveal that (i) the small displacements in the reversed direction are a more powerful stimulus than the sector motion in the forward direction, (ii) the effect can be seen only if the spoke width is small (< 5 min of arc) when the stimulus is viewed foveally, and (iii) the asynchronous movements of the spokes are seen as being distributed uniformly and synchronously over the whole display. These simple observations tell us something about the spatial and temporal characteristics of the human motion system.

5.3 Contrast Affects Motion Strength

It is well known that perceived speed can depend on contrast (Thompson, 1976, 1982; Campbell and Maffei, 1979, 1981; Kooi et al., 1992; Stone and Thompson, 1992; Hawken et al., 1994; Ledgeway and Smith, 1995; Gegenfurtner and Hawken, 1996; Smith and Derrington, 1996; Thompson et al., 1996; Thompson and Stone, 1997; Blakemore and Snowden, 1999). We have recently investigated five fresh examples of this contrast dependence, namely:

1. Motion strength: Time till breakdown
 2. Motion strength: Crossover motion
 3. Speed: The footsteps illusion
 4. Direction: The plaid-motion illusion
 5. Direction: Split dots
1. In *time till breakdown*, the strength of apparent motion depends on its contrast (Figure 5.2) and can be measured by timing its durability. A spot or bar that jumps back and forth between two positions gives an impression of apparent motion (AM), but prolonged inspection of the stimulus causes the initial impression of AM to degrade to flicker (Kolers, 1964; Anstis, Giaschi and Cogan, 1985). This adaptation effect was measured for a single jumping bar (Smith and Anstis, in press) and was found to depend on bar contrast; the time till breakdown TTB (the time at which the impression of AM first degraded into flicker) was greater for a higher-contrast bar and fell off as contrast was reduced, but it was independent of the bar's luminance polarity (Figure 5.3).



High contrast bars have longer TTBS than.....Low contrast bars.

FIGURE 5.2. Contrast bars

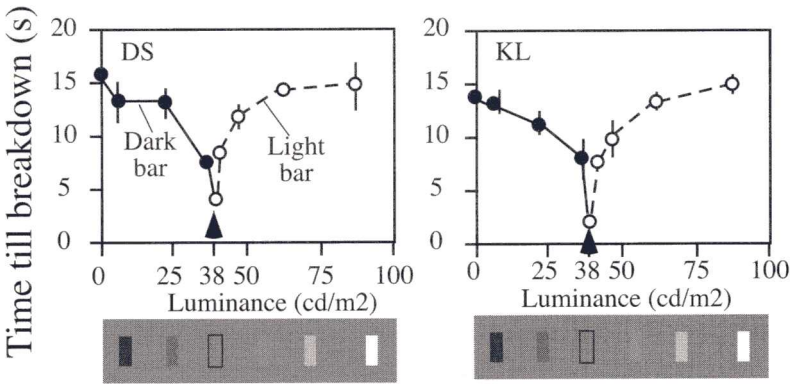


FIGURE 5.3. Graph shows that time till breakdown (TTB) increases with contrast, for bars either lighter or darker than the surround. Polarity does not matter.

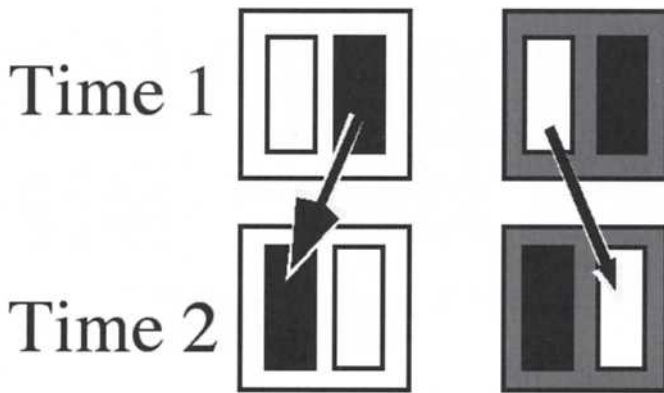


FIGURE 5.4. Crossover motion. A black and a white bar exchange luminances. On a light surround, the dark bar appears to jump. On a dark surround the white bar appears to jump. Thus, the bar with higher contrast has the stronger motion signal.

2. Another motion phenomenon that depends upon contrast is “crossover motion” (Anstis and Mather, 1985; Mather and Anstis, 1995; Anstis, Smith and Mather, 2000; Smith and Anstis, in press). Two parallel bars side by side, one dark and one light, switch luminances repetitively over time. This generates a stimulus that is consistent with two potential competing bar motions; one dark and the other light.

Whether observers see the light bar or the dark bar as moving depends critically on the luminances of the bars and their surround. On a dark surround, the light bar is seen as moving. On a light surround, the dark bar is seen as moving. The bar differing more from the surround luminance dominates the motion percept (Anstis and Mather, 1985).

- 1+2. *Time till breakdown for crossover motion.* After measuring the time till breakdown (TTB) for a single jumping bar, we measured the TTB for a crossover motion stimulus in which two bars, of different contrasts, jumped in opposite directions (Smith and Anstis, in press). A single jumping bar had a short TTB at low contrasts, and TTB grew longer as contrast increased. A single black bar had a long TTB (about 15 s at an alternation rate of 3.75 Hz). When a grey bar was added in opposite motion, creating a crossover stimulus, the TTB of the two combined bars was slightly shortened by a low-contrast opposing bar and was considerably shortened by a high-contrast opposing bar (Figure 5.5). Thus we measured the penalty (in terms of “strength” of apparent motion percept) that the winning motion signal paid in overcoming the simultaneous presence of the other motion signal. In short, TTB was a monotonic function of the *difference in contrast* between the two bars (Smith and Anstis, in press). For one bar’s motion to dominate the percept, the visual system must “discount” the motion of the competing bar. This discounting was not like a winner-take-all mecha-

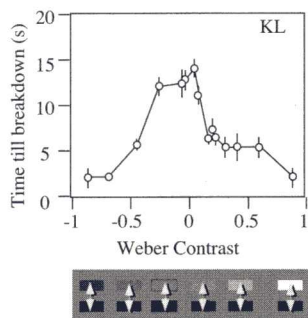


FIGURE 5.5. Competing opposite motions: Time till breakdown (TTB) for a black bar decreases when high-contrast crossover motion is added in the opposite direction. (Courtesy of David Smith.)

nism, in which the losing signal has no effect upon the dominating percept, but instead showed some inhibition from the losing signal. Winner-take-all would be like a horse race, in which the losing horses do not slow down the winner in any way, whereas the mutual inhibition that we discovered for TTB is like a tug of war in which the losers certainly impede the progress of the winners. Note that this motion inhibition pooled across both spatial decrements and increments.

3. In the “footsteps” illusion (Anstis, 2001) two grey squares, one light and one dark, move horizontally against a background of black and white vertical stripes (Figure 5.6). When the dark grey square moves across a white vertical stripe its edges have high contrast and it appears to speed up. When it moves across a black vertical stripe its edges have low contrast and it appears to slow down. The opposite is true for the light grey square. As a result the two squares appear to speed up and slow down in alternation, like the footsteps of a walking person. These changes in apparent speed are maximal for almost-white and almost-black squares, and they fall to zero for a mid-grey square.

This mid-grey lay at the arithmetic mean, not the geometric mean, of the black and white stripes. Thus if the black and white stripes had relative luminances of 1% and 100%, the footsteps illusion went away for a grey bar of luminance 50.5%, not 10%. At first this seems inconsistent with the well-known fact that the visual system applies a log transform to luminance stimuli. But we noted that a 50.5% mid-grey square had the same Weber contrast on the black surround as on a white surround, and we concluded that the apparent speed depended upon Weber contrast. (The mid-grey square had a Weber contrast of $(50.5 - 1)/50.5 = +0.98$ on a black surround, and $(50.5 - 100)/50.5 = -0.98$ on a white surround).

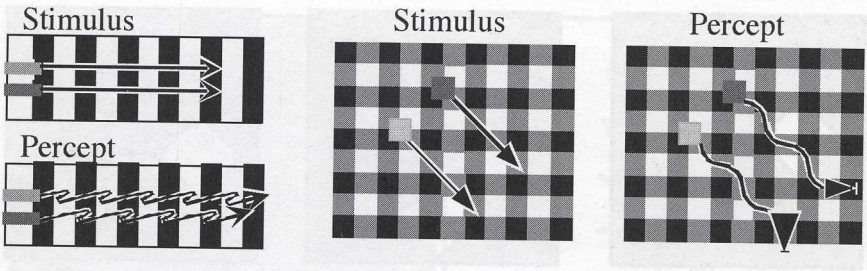


FIGURE 5.6. Artist's impression of the footsteps and plaid illusions. (2-D speed changes on plaid can change perceived directions.) See text.

4. *The plaid-motion illusion.* This was simply a 2-D version of the footsteps illusion. Two gratings were crossed to form a plaid that tiled the background with black, white, and grey squares. The two moving squares, one light grey and the other dark grey, were the same size as the plaid tiles. They moved in synchrony along parallel oblique paths at 45 deg to the orientation of the plaid (Figure 5.6b), but subjectively they appeared to wiggle in and out toward each other, changing their directions repetitively as they pursued their common oblique path (Figure 5.6c). To understand why, consider a light square moving down to the right, at the instant when it crossed over a “corner” of the plaid. When its leading right-hand edge moved on to black, the rightward motion of the square appeared to speed, because of the high contrast of the square’s leading edge. At the same instant its leading edge at the bottom moved on to white, so the downward motion of the square appeared to slow down because of the low contrast of the square’s bottom leading edge. Consequently the square seemed to veer toward the horizontal. When the light grey square moved across the next “corner” of the plaid, which had opposite luminance polarities, it seemed to veer toward the vertical. Corresponding arguments apply to the light square. As a result the two squares appeared to move along counterphasing wiggly paths.

5. *Split moving dots* In crossover motion, bars of different contrast moved in opposite directions. Our split-dot effects will now show that two combined orthogonal motions of different contrasts appear to move in a direction that is a function of the relative contrasts. Our time till breakdown (TTB) experiments established that two opposed motions (at 180° to each other) mutually inhibited each other in a kind of tug of war. Now imagine a peculiar tug of war in which two teams of unequal strength are pulling at right angles, with the stronger team pulling north while the weaker team pulls west. The rope would move at some intermediate angle such as north-northwest. Hiro Ito and I have found that when two dots of different contrasts cross each other at right angles, they can combine into a single vector, or perceived direction of motion. This vector gives a sensitive measure of the relative motion strengths of the two dots.

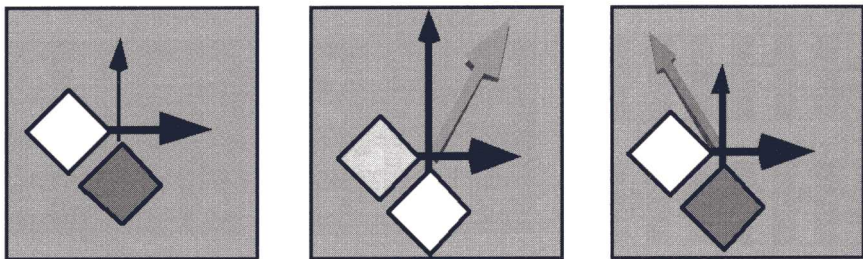


FIGURE 5.7. (left panel) Basic stimulus was two dots that crossed. (center panel) Vector summation of two dots of same polarity gave oblique motion (grey arrow), favoring dot of higher contrast. (right panel) Vector summation of two dots of opposite polarity gave perceived direction (dark grey arrow) outside the range of the two stimulus motions.

The dots in each pair were adjacent and touching, because Qian, Andersen and Adelson (1994a, b, c) showed that when fields of random dots drift over each other they separate out into sheets moving in different directions, so-called “transparent” motion. It is only if dots are arranged in touching pairs that they fuse together to give the “coherent” motion that we want. Braddick (1997) and Curran and Braddick (2000) have found that the visual system extracts the vector sum of these fused coherent dots in assigning a perceived direction, and we entirely agree. Unlike these authors, we were primarily interested in the effects of contrast upon the direction of perceived movement.

The basic stimulus was a pair of touching dots that moved along crossing, orthogonal paths (Figure 5.7). One dot jumped back and forth horizontally, whilst at the same instant the other dot jumped back and forth vertically. The dots had luminance values ranging from 4% (black) to 100% (white) on a 50% (mid-grey) surround. This gave to the dots Weber contrasts ranging from -0.6 (spatial decrements) to +0.6 (spatial increments). Luminances of the horizontally moving dots are shown on the abscissa, and of the vertically moving dots on the ordinate.

Ito and I set up a 7×7 array of dot pairs, and observers were invited to set a line to match the perceived direction of each of the 49 dot pairs. Results are shown in Figure 5.8b. Broadly speaking, the perceived directions radiate out from the center of the graph. We treated the orientation of each motion arrow drawn by the observer as the vector sum of a horizontal and a vertical motion, and the length of each of these vectors is taken as an index of its relative motion strength. In summary, we found that perceived motion strength varied linearly with contrast, for dots of the same polarity. The same linear law was true if the dots had opposite polarity, with one dot being lighter than the grey surround and the other darker; but now the contrast of the decremental dot had to be taken as a negative number.

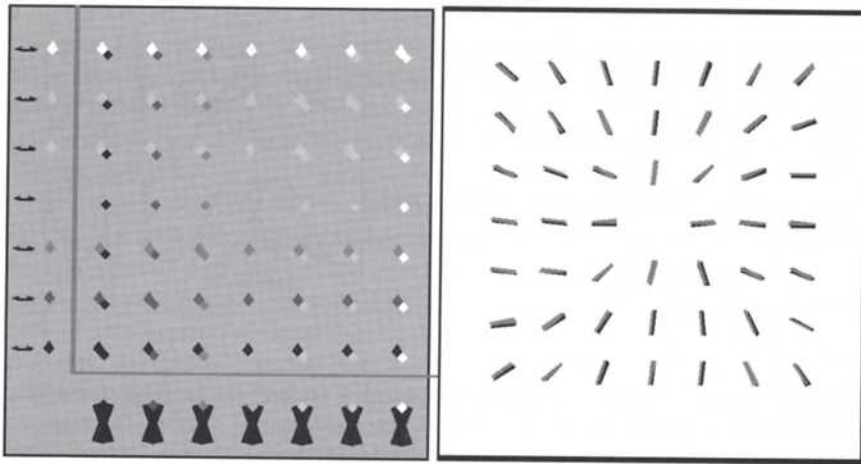


FIGURE 5.8. (left panel) Split-dot display comprises pairs of dots that jump back and forth, as in Figure 5.7. Luminance of horizontally jumping dots is shown on x -axis, and of vertically jumping dots on the y -axis. (right panel) Perceived directions of motion show vector summation and differencing of dots with different contrasts.

To summarize, our experiments show that contrast affects motion strength and apparent speed. Contrast increases motion strength, or resistance to breakdown into flicker, as measured by time till breakdown (TTB). In crossover motion there is a contest between two potential motions in opposite directions (at 180 deg to each other), and the higher contrast wins. However, the net strength of the winning motion is reduced because the losing motion of the other bar is subtracted from it — so the situation resembles a tug of war more than a horse race. We demonstrated this reduction in net strength in our time till breakdown experiments. In our split-dot motion experiments we found that the visual system takes the vector sum of two orthogonal motions, as weighted by their relative contrasts. In the footsteps illusions, contrast affects perceived speed of a drifting square. When a background plaid generates two orthogonal footsteps illusions, alternating over time, the relative motion strengths are expressed as changes in direction of the drifting square. Finally in the peripheral-oblique illusion, the center and terminators of a line are in competition, and the relative visibility of the center and the ends, as determined by the line's contrast, determines the perceived net direction.

5.3.1 Contrast and Motion: Conclusions

- High-contrast motion looks faster, and is more durable, than low-contrast motion.
- Speed changes are local in space and time (in the footsteps illusion)

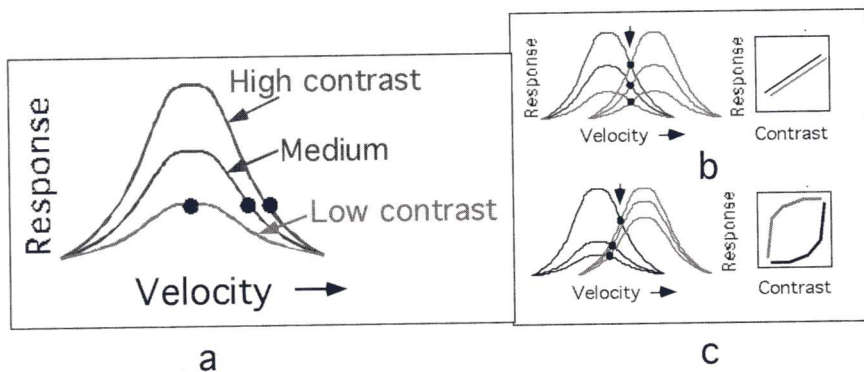


FIGURE 5.9. (a) A hypothetical cell in MT, tuned to velocity but sensitive to contrast, would confound three stimuli (spots) of different velocities and contrast. (b) Adding a second unit tuned to higher velocities would disambiguate velocity from contrast. Three stimuli (spots) of the same velocity but of different contrasts, would evoke the same firing ratio (here 1:1) from the two units. (c) However, nonlinear responses to contrast in the two units could allow contrast to distort the velocity signals again.

- 2-D speed changes (across a plaid) can change perceived directions
- Split dots, whether of the same or opposite polarities, give motion signals proportional to their contrast.
- These dot motions are combined by vector summation

What kind of visual codes for motion will be susceptible to distortion by stimulus contrast? One simple candidate code would *totally* confound contrast and velocity. Consider a visual neuron in MT that is tuned to a preferred range of velocities, as described by Maunsell and van Essen (1983). The response of such cells also depends upon stimulus contrast (Sclar and Freeman, 1982), so the *hypothetical* responses of such a cell to velocity and contrast are diagrammed in Figure 5.9. The cell would give a maximum response to a high-contrast stimulus moving at its preferred velocity, and would be less responsive to higher or lower velocities. Its response would also fall when the stimulus contrast was reduced. Figure 5.9a shows three hypothetical stimuli of different velocities and contrasts. The left-hand spot shows a low-contrast stimulus moving at the unit's rather slow preferred velocity. The right-hand spot shows a stimulus of high contrast but moving faster than the unit prefers. The middle spot is in between. All three spots have the same vertical height; in other words, they all elicit the same firing rate from the unit. By the principle of univariance (Estevez and Spekreijse, 1982) the firing rate of a neuron cannot distinguish between a low-contrast stimulus at the preferred velocity from a high-contrast stimulus at a less-preferred velocity.

This problem of confounding velocity with contrast can be solved by adding additional tuned units (Figure 5.9b, c). In this figure the three spots show three stimuli of the same velocity but of different contrasts. A single tuned unit responds differently to all three. However, the addition of a second unit tuned to

a higher preferred velocity disambiguates the stimulus. All three stimuli provoke the same ratio of firing between the two units, and this is the velocity code. A higher contrast makes both units fire more rapidly, but their ratio of firing is preserved (Figure 5.9b). This is similar to the coding of hue by three broadly tuned retinal cones, and is one of the class of models known as banks of tuned filters (Regan, 2000).

All is well, provided that everything is linear. But suppose that the gamma, or contrast response, of the two hypothetical units is different. The result will be that velocity and contrast are again confounded (Figure 5.9c), although not on the wholesale scale committed by a single tuned unit. I conjecture that this type of nonlinearity is responsible for the illusory changes in apparent speed produced by changes in contrast. Note that this dependence of motion on contrast as a motion analog of the Bezold-Brücke hue shift. When spectral light increases in luminance, the hues change. Normally, long-wavelength light becomes increasingly yellow, and short-wavelength light turns blue or blue-green. This is caused mainly by nonlinear responses of colour-opponent P cells in the retina (Ejima and Takahashi, 1984) and in the lateral geniculate nucleus (Valberg, Lange-Malecki and Seim, 1991). Note that in the Bezold-Brücke phenomenon, x = luminance, y = hue, whilst in our effects x = contrast, y = strength of motion signal.

So far we have shown that low-level motion signals increase as the stimulus contrast increases. Of course, this gives rise to perceptual errors. Its advantage may be that increases in contrast increase the salience, and hence the perceived reliability, of motion signals at the expense of an accurate representation of absolute speed (Clifford and Wenderoth, 1999).

5.4 From Low-Level to High-Level

So far we have shown that low-level neural motion signals are considerably distorted (increased) as the stimulus contrast increases. We turn now to high-level processes whose job is integrate these signals into the perception of moving objects. For instance, each side of a moving polygon generates local motion signals that are usually different from the direction in which the whole polygon moves — the so-called “aperture problem.” We are perversely interested in partial and complete failures in high-level solutions of the aperture problem. Moving line terminators help to solve the aperture problem, but these solutions are modified by stimulus contrast in the plaid-motion illusion and in the peripheral-oblique illusion. Thus, perceptual combinations of contrast-distorted motion signals lead to distorted trajectories for moving objects — a minor failing. We also recapitulate our “chopstick” illusion (Anstis, 1990) and “sliding rings” illusion, in which the motion of terminators propagates along straight lines and is blindly (and incorrectly) assigned to the motion of the central intersection. Both illusions show grossly erroneous integration of line motions and terminators — an almost complete failure.

5.5 Terminators and the Aperture Problem

The motion of a long straight line is ambiguous if its ends are hidden — for example when an observer views it through a round aperture — or when it passes across the round receptive field of a motion-sensitive neuron. The line is invariant under translation along its own length, so its motion is ambiguous, and oblique motion cannot be discriminated from orthogonal (Adelson and Movshon, 1982; Movshon et al., 1983; Hildreth, 1983; Wilson, 1994; Shiffrar and Pavel, 1991; Lorenceau and Shiffrar, 1992; Duncan, Albright and Stoner, 2000). This is the aperture problem. A vertical line that moves to the right gives the same retinal stimulus whether it be moving to the right, or up-to-the-right, or down-to-the-right. (The difficulty arises not from the aperture itself but from the fact that the ends of the lines are not seen, so it should really be called the “endless problem”). This raises the problem of how we can correctly see a moving square. Adelson and Movshon (1982) suggested that a vertical line is constrained to move along any of the set of arrows shown in Figure 5.10a in order to reach its right-hand position. If this is the right-hand side of a square that is moving obliquely down to the right, the bottom edge of the same square undergoes a similar set of constraints that make it move vertically down, or obliquely down (Figure 5.10b). The point at which these two constraint lines intersect (Figure 5.10b) defines the true direction of motion, namely at 45 deg down and to the right.

5.6 Contrast Affects the Aperture Problem: The Plaid-Motion Illusion and Intersections of Constraints

A plaid surround can induce 2-D illusions that change the apparent direction, not just the speed, of moving squares (Anstis, 2001). A plaid was made by superimposing two orthogonal square wave gratings, and a light grey square and a dark grey square drifted obliquely across the plaid. Result: Although the squares followed parallel paths they appeared to vary in direction, seemingly moving in and out toward and away from each other. Consider a light grey square lying on a plaid and jumping back and forth obliquely at 45 deg to the vertical (Figure 5.10). The square has black on either side of it, which enhances its horizontal motion, and it has white above and below it, which de-emphasise its vertical motion. Consequently the light grey square appears to veer toward the horizontal. For corresponding reasons a dark grey square (not shown) appears to veer toward the horizontal.

Contrast acts here in a dynamic fashion, rotating the perceived trajectory of a moving object without perceptually displacing the contours of a stationary object. Contrast subjectively enhances the amplitude of the horizontal motion component and reduces that of the vertical motion (Figure 5.11c), shifting the intersection-of-constraints solution toward the horizontal. It follows that contrast modifies the

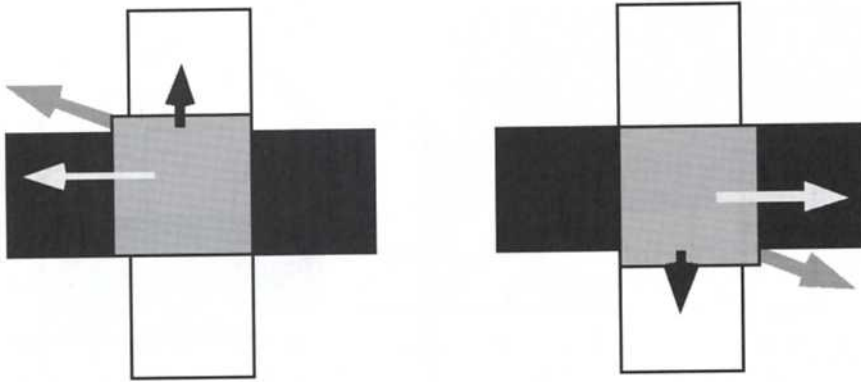


FIGURE 5.10. Explanation of the plaid illusions illustrated in Figure 5.6. When a light grey square makes small back and forth jumps on a black/white plaid, its left and right edges have high contrast against the black surround, which enhances the horizontal component of motion. Its top and bottom edges have low contrast against the white surround, which de-emphasises the vertical component of motion. Result: the oblique motion looks somewhat horizontal.

amplitude of perceived motion before the intersection of constraints is computed (Adelson and Movshon, 1982).

5.7 Contrast Affects the Aperture Problem: The Peripheral-Oblique Illusion

I stumbled by chance on another illusory phenomenon in which stimulus contrast determines the solution to the aperture problem. Faced with the ambiguity of a straight line moving behind an aperture, the default percept is that the line moves at right angles to its own orientation. The line's motion is completely disambiguated if the terminators, or ends of the line, are visible. Then the default solution to the aperture problem is rejected and the motion of the terminators propagates along the whole line, which is seen correctly as moving in the same direction as its terminators. I have found that an aperture problem can arise even without an aperture! Figure 5.12 (top icon on left) depicts a white or grey line, tilted at 45 deg from vertical and moving vertically up and down through a distance of 6 deg at a rate of 1 Hz. The line is 6 deg in length and is viewed with both eyes against a black background at an eccentricity of 15 deg, with strict fixation. Usually the line is correctly seen as moving vertically. However, if the line is made really dim its trajectory appears to veer round toward the oblique, and by the time it is just above threshold it appears to move at 45 deg, at right angles to its own orientation.

At first I thought this was some kind of dark-adaptation effect, perhaps related to Pulfrich's pendulum. But this idea was quickly proved wrong when the line was

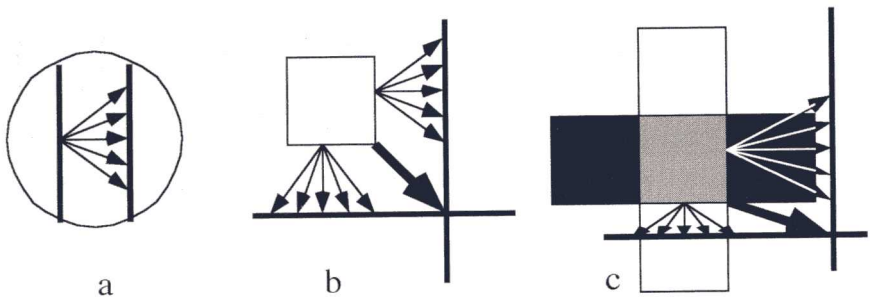


FIGURE 5.11. (a) In the aperture problem the motion of a long straight line seen through a round aperture is ambiguous and could be in the direction of any of the arrows. (b) So how is the moving square seen unambiguously? Adelson and Movshon's (1982) intersection of constraints solution. The thick vertical and horizontal lines form the "envelopes" of possible motions of the right-hand and bottom edges of the square. Their intersection point (bottom right) yields the perceived direction of the square. (c) When the motions of the sides of a square (taken from Figure 5.10) are distorted by contrast, the square's trajectory is distorted. Conclusion: Local neural signals from moving edges undergo contrast distortion before being integrated by intersecting constraints.

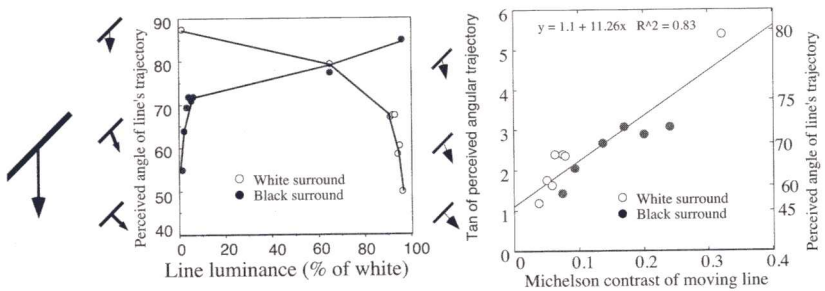


FIGURE 5.12. Perceived direction of tilted line moving in the periphery is veridical (vertical) at high contrast, but driven by motion of line center (obliquely) at low contrast.

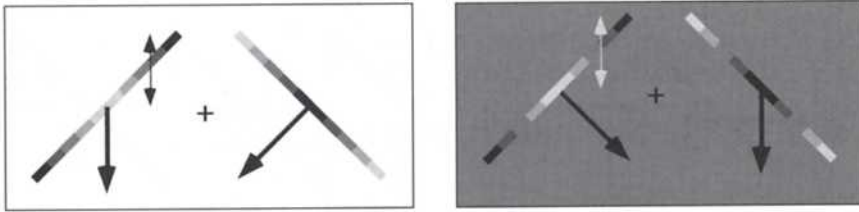


FIGURE 5.13. Spatially graded lines appear to move veridically (vertically) if tips have high contrast, but driven by center (obliquely) if tips have low contrast.

put on a white background. Now a black or dark grey line was seen veridically, and it was an almost-white line that appeared to veer toward 45 deg (Figure 5.12). It was the contrast of the line, not its luminance, that determined its perceived direction of motion. I replotted the lines as a function of their Michelson contrast,

$$abs[(L_{line} - L_{surround}) / (L_{line} + L_{surround})]$$

an expression whose value lies between 0 and 1. This made it clear that regardless of polarity a high-contrast line was seen veridically, whilst a low-contrast line was seen moving at right angles to its own length — almost as though it were being viewed through a nonexistent aperture.

I believe that at low contrast and in peripheral vision the terminators start to lose visibility, and with it their ability to influence the perceived direction of motion. Thus, the visual system's ability to solve the aperture problem depends upon the terminators reaching some criterion level of contrast; otherwise they are ignored. To verify this hypothesis I emphasised or de-emphasised the terminators in two moving, spatially graded lines (Figure 5.13). The left-hand line was black at both ends, shading to white at its center. The right-hand line was white at both ends, shading to black at its center. The lines were tilted at +45 deg and -45 deg, and both lines moved vertically up and down in step, on either side of a fixation point. Result: On a white surround, the trajectory of the black-tipped line was seen veridically as vertical, but the trajectory of the white-tipped line showed an illusory inclination (thick arrows in Figure 5.12). On a black surround the opposite was the case. Thus, on both surrounds and regardless of polarity, high-contrast terminators successfully disambiguated the motion, but low-contrast terminators did not.

What difference does eccentricity make? It seems to reduce the visibility of the whole line, in such a way that a low-contrast terminator is not seen clearly in peripheral vision, so it loses its influence on the perceived motion of its line. Why should the terminator be less visible than the rest of the line? Perhaps it is under-sampled, stimulating only one receptive field whilst the central portion of the line has a chance to stimulate a whole row of receptive fields.

Conversely, there is also something special about foveal viewing. In Figure 5.14 an oblique line moves vertically up and down past three stationary dots *j*, *k*, *l*. If one fixates *j*, positioned 1 deg to the left of the line, then the line is seen veridically as moving up and down. But when *k* is fixated, the central part of the line takes on

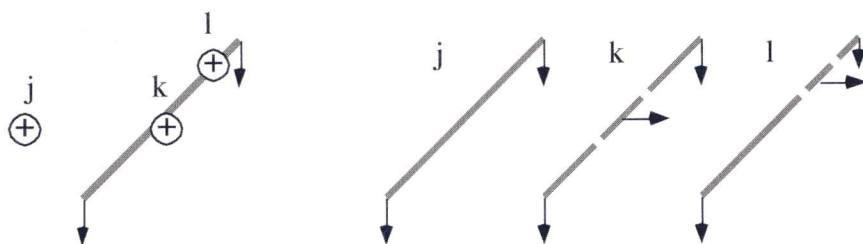


FIGURE 5.14. Oblique line moving downward. The portion near the fixation point appears to move locally to the right.

a life of its own and seems to move horizontally as it passed through *k*. This effect is tied to the foveal location and is not merely a landmark effect, because when point *l* is fixated the portion of the line close to the new fixation point *l* appears to move horizontally.

5.8 Sliding Rods and Rings: The Chopstick Illusion

A long line that moves behind a circular aperture is invariant under translation along its own length, so its motion is ambiguous, and oblique motion cannot be discriminated from orthogonal. This is the aperture problem. Similarly, a circle is invariant under rotation. These invariances can produce strong illusions in the *sliding movements of intersections*. Steve Shimozaki and Dana Ballard from the University of Rochester and I have studied two motion illusions of this kind that reveal links between human perceptual representations and the motor system. In the “chopsticks illusion” (Anstis, 1990) a vertical and a horizontal line overlapped to form a cross, and each line moved along a separate counterclockwise circular path in antiphase, without changing orientation. The intersection of the lines moved clockwise, but it was wrongly perceived as rotating counterclockwise. In the “sliding rings illusion” two rings overlapped in a figure-8 and rotated about the centre of the figure-8. When two dots were added that rotated with the rings, observers reported seeing the two rings as welded together into a rigid 8. Observers could readily track the intersections of the rings. When each dot “floated” so that it lay at 12 o’clock on its ring, observers saw the figure as breaking into two separate rings that slid over each other, and the eyes were unable to track the moving intersections. We conclude that pursuit eye movements are under top-down control and are compelled to rely upon perceptual interpretation of objects.

Not all motions are visible; in particular, the sliding movements of intersections. The oblique motion of an arm sweeping past a horizontal table edge is clearly seen, but the horizontal motion of the intersection of the arm and table edge is never noticed. Yet the same retinal signal of two intersecting edges in some other context could easily give a sensation of motion. We suggest that observers parse intersections as being non-objects and therefore cannot see them

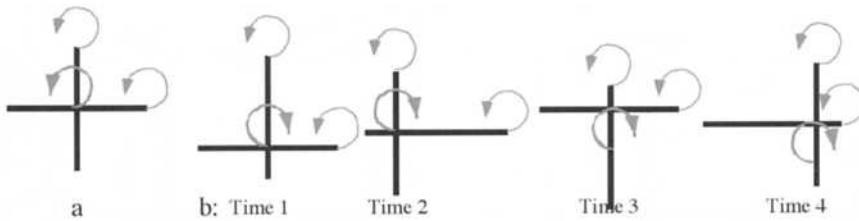


FIGURE 5.15. (a) A rigid cross that follows a counterclockwise circular path is seen veridically. (b) In the chopstick illusion, both rods follow similar counterclockwise paths but with a phase lag between them. Result: The central sliding intersection actually moves clockwise but appears to move counterclockwise. Conclusion: The motion of the line terminators is blindly assigned to the intersection.

move.

We studied intersections as follows. In Figure 5.15a, a cross moves clockwise along a circular “polishing” path, remaining upright like a sponge in the hand of a window cleaner. This control stimulus is always seen veridically. In Figure 5.15b two intersecting rods, one vertical and one horizontal, move clockwise along circular paths, forming a cross with the ends of the rods always visible (Anstis, 1990). The rods move in antiphase so that when the vertical rod is at 12 o’clock on its path the horizontal rod is at 6 o’clock. The central intersection of the two rods actually moves along a counterclockwise path (a Lissajou circle). The motions of these intersections were grossly misperceived. 230 undergraduates viewed videotapes of Figures 5.15a and 5.15b, rotating for 5 s at 2.2 rev/s. In both cases the center moved along exactly the same circular path; only the lengths of the arms changed over time. The control cross in Figure 5.14a was correctly seen as rotating clockwise by 99.6% of the students. Yet 86.8% of students incorrectly reported the center of Figure 5.15b as rotating clockwise, even though it actually moved counterclockwise. Thus they appeared virtually blind to the true motion of the center, and instead wrongly perceived it as moving along the same path as the tips of the rods. The visual system did not parse the sliding intersection as an object, and so refused to perceive its motion directly. Instead, it inferred the intersection’s path through space by monitoring the unambiguous clockwise rotation of the terminators (tips) of the rods. This tip motion propagated along the entire length of the rods and was blindly assigned to their intersection. We conclude that intersections were not parsed as objects, and therefore their motion path was not extracted, but instead the motion of the terminators (tips) propagated along the lines and was blindly assigned to the intersection.

Surprisingly, the chopstick illusion still persists if the two rotating rods have their ends clipped by a stationary square window or hole cut in a large, invisible screen. This means that the ends of the vertical rod move back and forth horizontally, and the ends of the horizontal rod move back and forth vertically. Because of the phase lag between the two lines, the center is still rotating counterclockwise — yet it still appears to be rotating clockwise! I am not yet sure why. However, when the aperture is made visible in Figure 5.16b, like a square hole cut in a tex-

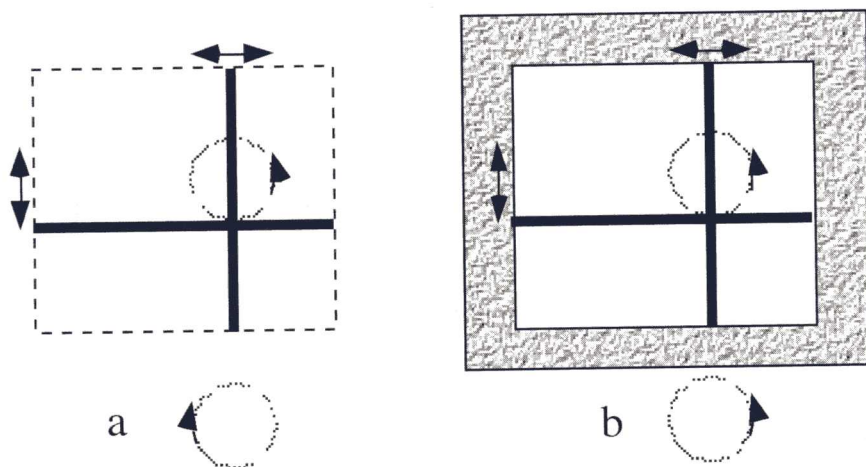


FIGURE 5.16. **a**, Chopstick illusion is still seen even when the tips of the lines travel along straight lines. **b**, Chopstick illusion vanishes. Extrinsic terminators behind screen permit veridical perception.

tured card, the two rods no longer appear to slide over each other, but immediately look like the rigid cross of Figure 5.16a moving coherently counterclockwise. The ends of the rods were perceived as extrinsic, that is, as occluded by the aperture and extending behind it (Shimojo, Silverman and Nakayama, 1989; Duncan, Albright and Stoner, 2000), and do not influence the perceived motion of the central intersection.

We recorded the eye movements of a naive observer when he attempted track the intersection of the two rods in Figure 5.15a and 5.15b with his eyes. The tracking errors during 20 stimulus revolutions, expressed as the mean deviation or offset between eye and target, were 1.06 deg of visual angle for the rigid rotating cross of Figure 5.15a and 5.6 deg for the chopstick illusion of Figure 5.15b, so the eye tracking errors were four to five times higher for the sliding than the rigid rods.

We then removed the terminators by bending each rod around into a smooth, featureless circular ring. The two rings overlapped to form a figure-8 and rotated at 1.25 rev/s about the center of the 8 (Figure 5.16c). Since each ring was invariant under rotation the figure-8 display was potentially ambiguous, being equally consistent with the two rings sliding over each other or else being welded into a single figure-8.

Four small marks were now placed on each ring, at 3, 6, 9, and 12 o'clock. This provided small cues that radically altered the perceived rotation.

1. Rings marked as in Figure 5.17a were perceived as a rigid welded figure-8, rotating coherently. This satisfies the rigidity constraint 10.
2. Rings marked as in Figure 5.17b were perceived as two separate rings, each remaining upright and sliding over its companion. Thus, perceptual rigidity

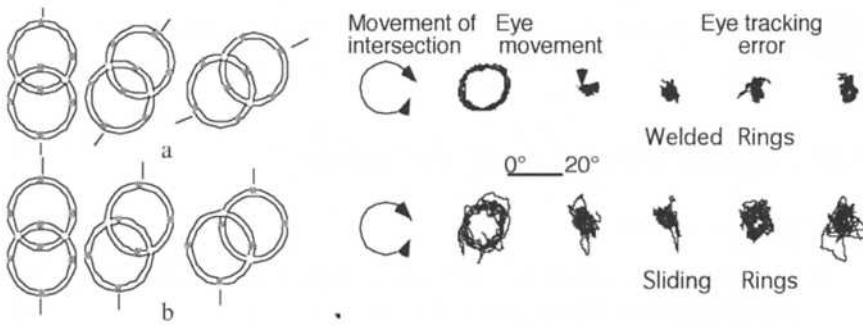


FIGURE 5.17. Two rotating rings overlapped in a figure-8. Short lines indicate the perceived rotation. (a) Rings appeared to rotate rigidly like a welded figure-8. Moving intersections could be tracked easily and accurately. (b) Rings appeared to remain upright and slide over each other. Moving intersections were tracked poorly and inaccurately. (c) Without the four marks on each ring, the rings appeared to slide as in part b, showing that motion perception aimed at minimising local motions, not at conserving rigidity.

was sacrificed in favour of minimising the motion seen within each ring.

Unmarked, featureless rings (not shown) often appear to slide over each other, especially if the rings lay in different planes of stereo depth. This shows that the visual system preferred to minimise local motions within rings rather than to maximise global rigidity of the whole 8 (Ullman, 1979; Braunstein and Andersen, 1984). It cannot be predicted from the vague idea that the visual system prefers "simplicity" or a "good Gestalt". We found that perceptual organisation of the stimuli strongly affected pursuit eye movements. The observer was asked to track the intersection of the two rings in Figure 5.17a or 17b with his eyes. The tracking errors for four observers during 20 stimulus revolutions are shown to the right of the stimuli. The rings of Figure 5.17a, which were seen as a rigid figure-8, were tracked accurately with a mean deviation error of only 1.04 deg of visual angle. However, the rings in Figure 5.17b, which were seen as two rings sliding over each other, gave a mean deviation of 9.93 deg, so the eye tracking error was 9.5 times higher for sliding than for welded rings. This breakdown in tracking performance as a result of a small change in stimulus markings has the surprising implication that smooth pursuit movements, which are normally thought of as a bottom-up servo system based upon retinal feedback (Lisberger, Morris and Tychsen, 1987; Krauzlis, 1994) may be strongly influenced by top-down cognitive processes such as object interpretation (Kowler, 1990).

Thus, although a moving stimulus is usually necessary to initiate smooth voluntary pursuit movements (Ullman, 1979; Braunstein and Andersen, 1984; Lisberger et al., 1987) it is not always sufficient. A welded intersection could readily be pursued but a sliding intersection could not, even though the foveal stimulus was identical and the peripheral retinal stimulus nearly so in the two cases. The essential difference lies not in the details of the retinal stimulation but in the higher level cognitive parsing of the objects represented by this retinal image; top-down

cognitive processes played a role in enabling or disabling pursuit eye movements.

5.9 Aperture Problem: Conclusions

- Terminators rule!
- They disambiguate motion of line centre (intersection of constraints) — but after contrast has altered perceived motion.
- Chopstick illusion: Motion of terminators blindly assigned to centre ...
- ... but not if ends of lines are hidden (extrinsic terminators).
- Intersections are not parsed as objects, and eyes can't track them.
- Dim peripheral terminators do not affect seen motion.

5.10 One Low-Level Stimulus, Two High-Level Interpretations: Local Versus Global Perception of Ambiguous Motion Displays

We have seen how the ambiguous motion of a straight line is disambiguated by combining it with unambiguous motion of the line's terminators. This leads us on to a much more general question — how are motion signals in different parts of the visual field combined? An ideal visual system would successfully combine all the motion signals that arise from a single moving object, while segregating them from signals that arise from other moving objects (Curran and Braddick, 2000). The combination could be done by some kind of global organizing principles, but a local propagation process might achieve the same result more economically by combining adjacent moving regions, providing that the motion paths are similar enough to satisfy some criteria. In 1983, Ramachandran and I examined ambiguous dot quartets, in which the dots at top and bottom corners of an imaginary diamond are flashed up, then replaced by dots at the left and right corners. This is an ambiguous stimulus, in which the top dot is equally often perceived as jumping down to the left, or down to the right. We wondered what happened when a whole field of a dozen or more of these dot quartets was visible at once. Do all the dots move in step, or does each dot quartet follow its own whim, so that about half the top dots jump down to the left while the other half jump down to the right? We found a very strong tendency for all the dots to move in the same directions. This display is a dynamic analog of a set of reversible Necker cubes, where one can ask whether all the cubes reverse in step, or independently.

Alecia Dager and I have recently been studying a new multimotion display. A pair of dots rotates clockwise around a common center at 1 rev/sec. Four such

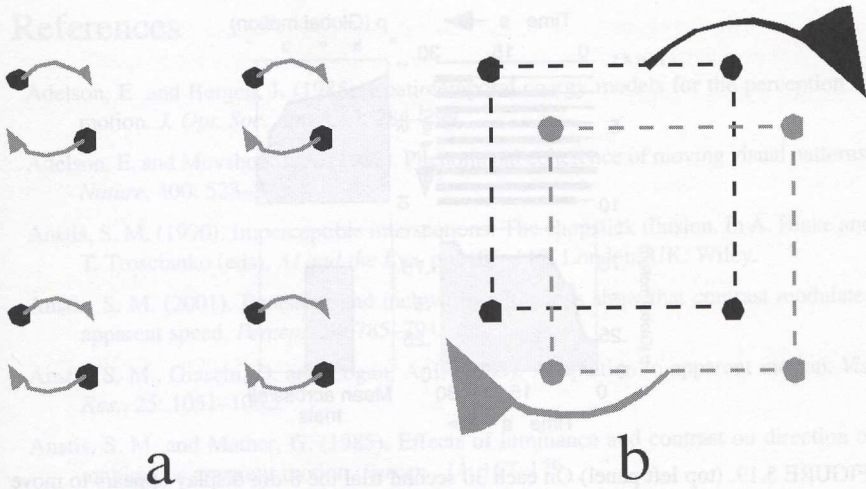


FIGURE 5.18. 8-dot display showing ambiguous binding. (a) At first it looks like four local pairs of dots, each rotating about a common center. (b) Same display looks like two large moving squares with a dot at each corner. Only the dots, not the arrows or dotted lines, were visible in the actual display.

pairs, well separated and rotating in synchrony, are arranged in a square array (Figure 5.18). At first each pair is seen rotating clockwise, but no interactions are seen between different pairs. In other words only “local” motions are perceived. But soon the display undergoes a radical perceptual reorganisation; the dots suddenly coalesce into two large, overlapping squares that slide over each other along circular paths without rotating, somewhat like a glass of water that one is rinsing out, or like the sponge in the hand of a window cleaner. We call this “global” motion. Thus, during local motion the observer sees four small pairs of rotating dots, whilst during global motion the same display looks like two large quartets of dots following a circular path. The display tended to flip back and forth over time between local and global motion, although the physical display never alters. In other words the ambiguity in this display lay not in the motions themselves, but in the perceptual groupings, or solutions that the visual system adopted to the “binding problem.”

We find that motion always looks local upon first viewing, but global motion tends to increase over time, both within a single trial and across a sequence of separate trials. Observers view the display for a period of 30 s, striking keys to indicate when they see local or global motion. Ten trials are run and then averaged together, second by second. The resulting average curve shows that the probability of seeing global motion increases steadily during the 30 s observation period. We also noted that the percentage of each successive 30 s trial for which seeing global motion was seen, increased from trial to trial. This suggests two separate perceptual processes, both favouring an increase in global motion, but with different time constants.

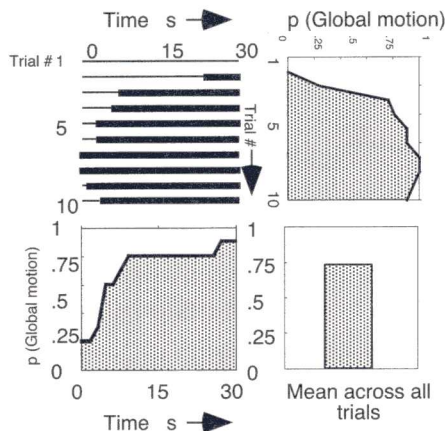


FIGURE 5.19. (top left panel) On each 30 second trial the 8-dot display appears to move locally (thin lines) or globally (thick lines). Ten trials averaged together (bottom left panel) show that probability of seeing global motion increases throughout the 30 second trial. Averaging each trial (top right panel) shows that global motion also increases from one trial to the next. Averaging across all times and trials (bottom right panel) shows that mean probability of seeing global motion was 0.75.

Shifting the display on to a fresh patch of retina restores local motion. Adding more pairs of dots increases the amount of global motion, but increasing the number of dots within a group from 2 to 3 to 4 has the opposite effect, making the display look more local. We also find that we can increase the amount of local or global motion by adding visible cues such as color that provide independent cues to grouping. Making both dots in one circling pair red and coloring another pair green, another pair blue, and so on, greatly increase the chances of seeing local motion. Conversely, making one dot in each circling pair red and the other dot green gives a large square of red dots and a large square of green dots. This greatly increases the chances of seeing global motion.

Local and global motion are two different and incompatible solutions to the problem of binding dots into groups. They are incompatible because it is impossible to see the same dots as partaking in local and global groups simultaneously. We suspect that local motion is preattentive, whereas global motion is attentive.

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