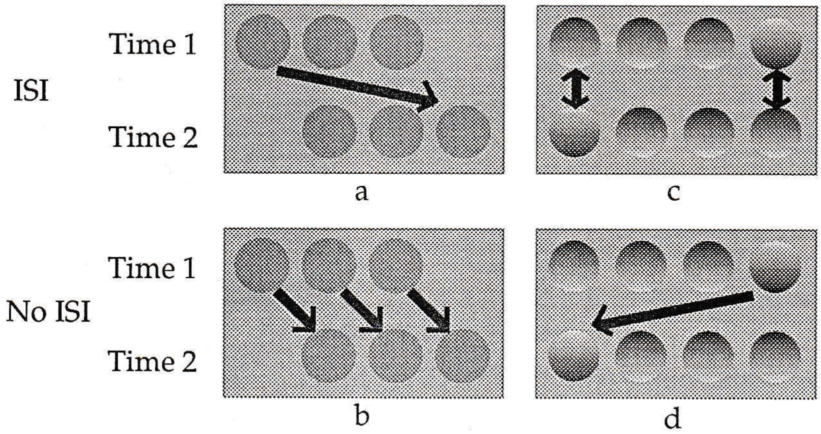

Figure 7 Ternus display.
a, with no ISI, element motion was seen, with the end disk jumping back and forth.
b, with an ISI, three disks jumped back and forth as a group.
c, with no ISI the shaded disks at the end flip up and down, driven by local luminance cues.
d, with an ISI the bump-like shaded disk jumps back and forth across three apparently stationary saucer-like disks (See Ramachandran 1988).

Figure 8 shows the effects of pitting two determinants of apparent motion against each other: luminance contrast, and the depth cue of covering. The visual system is confronted with the choice of either a low-level decision that the higher contrast object is moving, or else an intelligent decision that the nearer object is moving. In Fig. 8, two squares jumped back and forth, one in front of a barrier of wavy lines and the other behind it. The rear square was always held at a mid grey on a black background. The front square was either light grey, dark grey or mid grey.

When the front square was light grey, it was both seen in front of the other square because of the covering cue, and was also higher in contrast because it was lighter against the black surround. Result: not surprisingly, it seemed to be the square in motion when the two pictures were alternated.

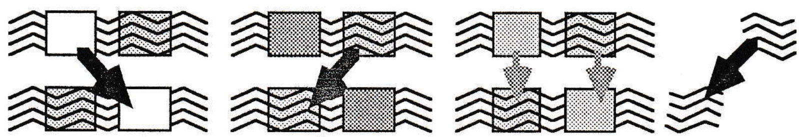

Figure 8 In these ambiguous motion displays luminance contrast was pitted against the depth cue of occlusion. The surround was black so the lighter squares had higher contrast.
a, Cues in harmony. The high-contrast light square was in front, covering the wavy lines, and it appeared to move (arrow).
b, Cues in conflict. Contrast won out over depth: the lighter, high-contrast square in back appeared to move (arrow), and the darker, low-contrast square in front did not.
c, Contrast cue minimal or absent. Squares had different hues but the same luminance throughout. Squares appeared stationary (grey arrows), but the wavy lines appeared to detach from the squares and jump back and forth independently, as diagrammed in **d.**

When the front square was dark grey, occlusion cues still identified it as lying in front of the other square but now it was lower in contrast. Result: contrast won out over depth, and the more distant, higher contrast mid grey square was the one that appeared to jump back and forth while the nearer, dark grey square appeared stationary. Thus the low-level luminance cue won out over the potentially "intelligent" depth interpretation.

It might be that contrast overcame depth not because contrast was strong but because depth was weak, being supported only by the cue of occlusion. Accordingly we added in stereo (not illustrated). The squares that covered the wavy lines in Fig. 8a, b (on the left at Time 1 and on the right at Time 2) were now also put in front of the wavy lines in stereo depth, and the other squares were put behind the wavy lines in stereo depth. This changed the motion percept. Now the squares no longer jumped sideways in the frontoparallel plane. Instead, each square jumped back and forth in depth along the line of sight, as in Fig. 6b.

When the two squares were set to different hues of the same luminance (or else both were set to the same mid-grey) and the two pictures were alternated, a most surprising result was observed (Fig. 8c, d): The two squares now flickered in colour at each alternation but did *not* appear to move, and the patch of wavy lines that lay in front of one square broke free of the remaining wavy lines to which it was hitherto firmly attached, and jumped across to lie in front of the other square.

This is reminiscent of the finding by Ramachandran and Anstis (1986) that figure-ground organisation can constrain apparent motion. An outline square jumped back and forth in front of a stationary random-dot surround (Fig. 9). The parts of the background that were covered and uncovered by the square looked stationary. Next, the outline was deleted so that only an empty region moved back and forth. The percept now changed radically; the previously moving square region now looked liked like two stationary empty holes, with a group of background dots jumping back and forth between them, even though the dots in the two background regions were uncorrelated. We conclude that the visual system normally suppresses spurious motion signals that are generated by covered and uncovered regions.

What parts of the motion system can be adapted?

As we move through the world the retinal image of objects ahead of us expands and the image of objects behind us contracts. We use this *optic flow* to guide locomotion (Cutting 1986: Koenderink 1986). We can use optic flow to assess the time to collision: there is evidence that long jumpers use it

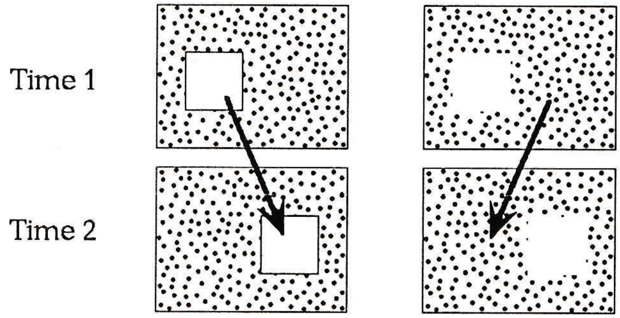

Figure 9 Occlusion and apparent motion (Ramachandran and Anstis 1986).
a, The outline square was perceived as jumping back and forth (arrow) against a stationary random-dot background.
b, when the outline was removed a group of dots, previously a stationary part of the background, appeared to jump back and forth (arrow).

to adjust their stride just before a jump (Lee 1980), and diving sea birds know from visual cues when to fold their wings just in time before they hit the water (Lee and Reddish 1981). Regan, Beverley and Cynader (1979) have discovered specialised visual channels that respond to size change. When confronted with an expanding square, local motion detectors first sense the outward motions of the opposite sides of the square, and then the size change detectors respond to the velocity difference, derived from the output of these motion detectors. The same authors also discovered visual channels that respond to motion in stereo depth.

Brian Rogers and I (in press) wondered whether there are also size change detectors that respond to change of spatial frequency content over time. The spatial frequency content of an approaching target zooms down the spatial-frequency spectrum, and this could be detected very rapidly by a hypothetical mechanism -- a type of "neural speedometer" --that received inputs from spatial frequency channels and detected gradual increases or decreases in spatial frequency. Such a frequency sweep detector could be very fast and computationally cheap because it would need merely to detect changes in the relative activity levels in different spatial frequency bandpass filters. Unlike local motion detectors, it would not need to discriminate spatial phase.

We tested this idea with two types of zooming random-dot texture display. One texture simply expanded repetitively. It looked like a movie made by aiming a movie camera at the centre of a sheet of stationary sandpaper and steadily zooming the lens in. The other texture also expanded repetitively, but whereas the texture grains grew gradually larger from frame to frame as before, the grains were replaced on every frame by a fresh set, with no frame-to-frame correlation between the grain positions. It looked like a movie made by shooting a single frame of a sheet of stationary sandpaper, then zooming the lens in slightly and using a *different* sheet of sandpaper on each successive frame. Stated differently, the stimulus consisted of twinkling dynamic random visual noise in which the mean grain size gradually expanded. So this stimulus provided expansion without correspondence between successive pattern elements.

Result: the coherently expanding texture gave a strong impression of motion, whereas the phase-jittered texture did not. Furthermore, following a 60-s adaptation period, the coherent stimulus gave a strong motion aftereffect but the phase-jittered stimulus gave none at all. We repeated the experiment with an expanding grating which either was, or was not, jittered randomly in phase. Results were the same as for the random noise: the simple expanding grating gave a strong percept of expansion, followed by a strong motion aftereffect, but the phase-jittered grating did not. The two stimuli had the same amplitude spectra over time, but differed in their phase spectra. In summary, we found no evidence for a rapidly acting, phase-blind channel that responds to temporal changes in frequency. Instead, our results could be explained by local motion detectors. Note that our results cast no doubt upon those of Regan et al. (1979) since our stimuli and conditions were very different.

Spatial phase spectrum is important for object recognition. One can dissociate the amplitude and phase spectra of a stationary stimulus, and once the spectra are dissociated, one can recombine the amplitude spectrum of one stimulus with the phase spectrum of another stimulus, thereby forming a new pattern. Piotrowski and Campbell (1982) created such hybrid patterns, combining the amplitude spectrum of a military tank with the phase spectrum of a face. The resulting pattern looked like a face

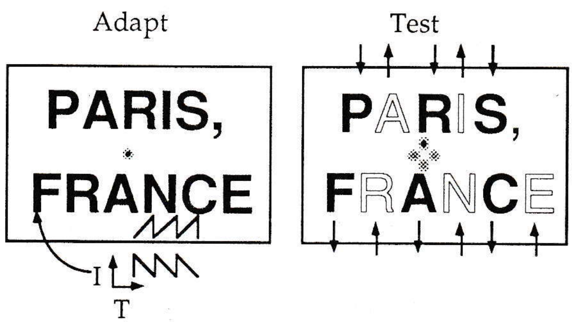

Figure 10 Motion aftereffects from motionless stimuli.
a, subjects adapted to dimming letters on a brightening surround, while fixating on the central spot.
b, subjects shifted their eyes to one of four fixation test spots, say the top one. Result: a motion aftereffect in which the light letters appeared to drift upwards, the dark letters downwards (arrows).

and not a tank. Piotrowski and Campbell also found that an image with the amplitudes of a face and the phases of a tank looked like a tank. They concluded that the phase spectrum of a stimulus was the primary determinant of its perceived identity. Our results suggest that spatial phase is just as important for perceiving the motion of a stimulus as it is for recognising objects.

We confirmed the low-level, luminance-based nature of the motion aftereffect by producing motion aftereffects from motionless stimuli (Anstis, in press). First, we generated a ramp aftereffect (Anstis 1967) by exposing our subjects to the display shown in Fig. 10a. The letters in the words PARIS, FRANCE repetitively dimmed over time, and the uniform grey background repetitively brightened over time. The luminance of the two regions were modulated by 1 Hz sawteeth in opposite directions. Following 30 s of adaptation the modulation was stopped, and subjects reported a ramp aftereffect in which the letters appeared to brighten gradually and the surround appeared to dim. Fixation was maintained throughout on a central fixation spot. Next, subjects re-adapted to the same stimulus for a further 30 s, but now the test stimulus was as shown in Fig. 10b. The surround was a fixed mid-grey; half the letters (P,R,S: F,A,C) were slightly darker than the surround and the other letters (A,I: R,N,E) were slightly lighter. The central fixation spot was replaced by four test fixation spots arranged in a diamond. When subjects shifted their eyes to the uppermost test spot, they perceived the dark letters as apparently drifting upwards in a motion afterefect, and the light letters as drifting downwards (vertical arrows in Fig. 10b). If they looked at the lower fixation spot the aftereffects were in the opposite direction. If they looked at the left (or right) fixation spot the light letters appeared to be drifting to the left and the dark letters the right (or vice versa). Thus, following adaptation to directionless dimming and brightening stimuli, subjects could change the direction of the motion aftereffect within a single test period simply by re-directing their gaze. These aftereffects were not artifacts from eye movements, but arose from superimposing a region of ramp aftereffect upon a slightly displaced luminance contour in the test field. We conclude that the output from luminance-change detectors provide an input into motion detectors, and that no hidden assumptions of any kind play a role in the motion aftereffects. Here we are examining the lowest possible level of motion detection.

Acknowledgments This research was supported by Grant A0260 from the Natural Science and Engineering Research Council of Canada (NSERC) and by research contract 9-97109 from Canadian National Defence. I thank my co-workers Patrick Cavanagh, Brian Rogers, and V. S. Ramachandran, some of whose work is described here; Suneeti Kaushal for her assistance; and Ian Howard for helpful discussions.

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