4

Experiments on motion aftereffects

Stuart Anstis

Dept of Psychology,
University of California at San Diego

4.1 Introduction

How are we able to see moving objects? One might think we see them because they really are moving. But the images projected on to the retina by such moving objects are only patches of light and colour that change over space and time, so how do we proceed from retinal spatiotemporal changes in luminance to seeing movement? A single receptor, looking through its own "keyhole" or receptive field at only one point in the world, could not possibly see movement. As an object passed by, the receptor would be able to sense changes over time but it could not assess the direction from which its keyhole was being covered and uncovered. It is necessary to compare signals from at least two points in time and in space, and this is exactly the function of a Reichardt motion detector (Reichardt, 1961). Two receptors with adjacent or overlapping receptive fields feed into a comparator (Figure 4.1a). The receptor outputs are filtered with the output of one receptor being delayed. The undelayed output from one receptor is correlated with the delayed output of the other, in this case by multiplication. If the time taken for the spot to move between the two receptors is equal to the internal delay there will be a maximum signal out of the correlator. An alternative scheme proposed by Barlow and Levick (1965) uses subtractive inhibition instead of multiplicative correlation. The advantage of multiplication is that it can handle two successive inputs that are of different contrasts. In practice, two motion units are wired up back to back, so that (say) leftward motion is subtracted from rightward motion (Figure 4.1b). Reichardt's original work was on insects, and electrophysiologists have since found motion-selective neural units in nearly every vertebrate species. See reviews by Berkley (1982), Mather (1994) and Snowden (1994).

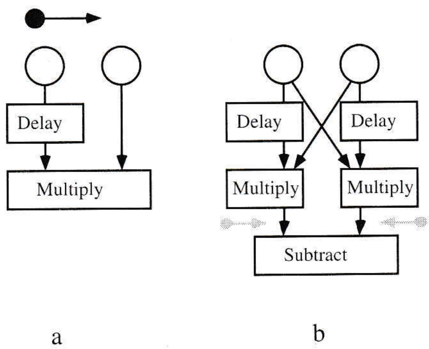

Fig. 4.1. a, Half a Reichardt motion detector. This responds only to a stimulus moving to the right. b, A Reichardt motion detector. This responds to motion to the left or to the right. c, A Reichardt detector must include a temporal filter that responds to change in luminance over time (see Experiment 1).

Adaptation to motion (say, downwards) alters the appearance of a subsequently viewed test motion in three different ways.

(i) Contrast threshold elevation. Downwards test motion is more difficult to see and must be increased in contrast to become visible. After prolonged inspection of a moving grating, Sekuler and Ganz (1963) found that the contrast threshold for a test grating moving in the same direction as the adapting grating was raised much more than for a grating moving in the opposite direction. This directionally selective adaptation was strong evidence that the moving target was detected by a motion-specific channel.

(ii) Motion aftereffect (MAE). This classic phenomenon was first reported by Aristotle (see Verstraten's review, 1996). First one adapts to a moving stimulus, say a waterfall. After 30 s of adaptation one transfers one's gaze to a stationary textured test field, which now appears to move upwards. This is attributed to adaptation of the downward branch of an up-down opponent Reichardt unit (Sutherland, 1961). A stationary field normally excites the upward and downward branches equally, so an opponent mechanism would signal no motion. However, exposure to downward motion adapts the downward branch, meaning that post-adaptation observation of stationary test field leads to an imbalance in which the up branch predominates. Consequently one sees the static test field apparently moving upwards. Barlow and Hill (1963) showed that a motion-sensitive neuron in the rabbit retina responded to motion less briskly after being exposed to prolonged motion in the cell's preferred direction.

(iii) Direction-selective adaptation. The direction of a test motion can be repelled away from the adapting motion. After adapting to downwards motion that moves toward 6 o'clock, a test field that actually moves toward 7 o'clock will appear to be moving toward 8 o'clock (Sekuler *et al.*, 1978). They concluded that the channels had broad petal-shaped receptive fields on a polar motion plot.

There are also two spatial interactions between motion pathways, which are spatial analogues to the temporal adaptation processes ii. and iii. just described:

(i) Simultaneous mutual repulsion of motion. Marshak and Sekuler (1979) and Mather and Moulden (1980) presented two overlapping sheets of sparse random dots. One set of dots moved (say) downwards, towards 6 o'clock, and the other set moved towards 7 o'clock. Subjects reported that the two directions appeared to repel each other so that the dots appeared to move towards 5 o'clock and 8 o'clock. The authors varied the angle between the two directions of motion and found a maximum repulsion effect of about 20^o when the two directions differed by 22.5^o. This 'motion contrast' is analogous to simultaneous brightness contrast, and has been explained as mutual inhibition between motion-sensitive pathways.

(ii) Induced motion. A static test field surrounded by downward motion appears to drift upwards. This is the classic induced motion effect (Duncker, 1929).

Muller and Greenlee (1994) examined the effects of adaptation to a drifting grating. They found three effects:

(i) It increased the lower velocity threshold of motion, that is, reduced sensitivity to very slow movement.

(ii) It shifted the point of subjective stationarity towards higher velocities of motion in the adapted direction. This confirms a result obtained by Sachtler and Zaidi (1993).

(iii) It increased the speed discrimination threshold for test contrasts below 0.1, having a maximal effect for adapting drift rates between 8 and 16 Hz.

4.2 My experiments

I shall describe six of my experiments on adaptation to motion which tell us a little more about the motion-sensitive pathways.

4.2.1 Motion aftereffects from ramp aftereffects

If one gazes steadily at a spatially uniform gray patch which grows gradually brighter [or dimmer], with its luminance modulated by a ramp or sawtooth waveform, then a subsequently viewed steady gray patch appears to be growing gradually dimmer [or brighter] (Anstis, 1967; Arnold & Anstis, 1993). This "ramp aftereffect" reveals the presence of adaptable visual pathways that respond selectively to gradual changes of luminance. This ramp aftereffect can be made to yield a motion aftereffect from motionless stimuli (Anstis, 1990), and this will show us that Reichardt motion detectors are also able to respond to gradual luminance change. First, notice that slow apparent motion can be produced from a stationary arrangement of two gray squares with a black line running down the border where they touch. If the left square gradually brightens while the right square gradually dims, the black line appears to move slowly to the right. Why? If the luminance profile is blurred, there is a gradual rightward shift in its peak. So any low-frequency visual pathways with large receptive fields will extract this luminance change over space and time, suggesting that motion can be sensed by very low-spatial-frequency pathways. The next step is to replace the physical luminance changes in the two squares with illusory changes produced by ramp aftereffects. The subject adapted to a dimming square on the left and a brightening square on the right. The two squares abutted but there was no black line along their join, so no apparent movement was seen. The squares were then set to steady gray and in the aftereffect the left square seemed to be dimming and the right square seemed to be brightening – but no motion was seen. Part way through the aftereffect, a black [or white] line was added along the join, and immediately it seemed to move to the right [or left] in an aftereffect of motion. So although there was no motion at any time in the adapting stimulus, a motion aftereffect was seen.

We do not even need the black line. Our next display was a mass of irregular blobs, half of them brightening and the remaining half dimming. All blobs abutted so there were no gaps between them. After 30 s of adaptation to this luminance change, the display was switched to steady blobs. If fixation was strictly maintained, ramp aftereffects were seen, with the previously brightening [dimming] blobs now apparently dimming [brightening]. But if fixation was shifted by a few min arc, the regions of aftereffect were now slightly displaced on the test stimulus. This had the same effect as drawing a contour a few min arc wide around the edges of the blobs. Subjects saw a clear aftereffect of motion – and if they changed their point of fixation, which displaced the slight offset between regions of aftereffect and the test blob, the motion aftereffect promptly changed its direction.

Since ramp aftereffects can be interpreted as motion aftereffects, we conclude that motion detectors include a filter to detect gradual change of luminance, dI/dT (Figure 4.1c).

4.2.2 Adaptation to back and forth apparent motion

Usually a motion aftereffect is produced by inspecting steady motion in one direction. This upsets the balance of an opponent motion detector. However, Debbie Giaschi, Alex Cogan and I (1985) have measured adaptation to back and forth apparent motion. A single spot that jumped back and forth in apparent motion between two positions in 'ping-pong' mode (Figure 4.2a) was at first seen as moving, but after a period of time the sensation of motion adapted out and was replaced by the impression of two dots flickering in place (Kolers, 1972). Some kind of phase or sequence information in the motion system has adapted out. The percept fluctuated irregularly over time between flicker and motion, but when we time- averaged over ten runs we found that the probability of seeing motion decayed exponentially over time. The faster the alternation rate, the weaker the motion signal and the more rapidly it degraded into apparent flicker. After an inspection of 30 s, a 3 Hz alternation still looked like motion for 44.4% of the time but a 4 Hz alternation for only 8.5% (Figure 4.2c).

This situation is really an adaptation experiment in which the adapting and test motions are identical. There are two reasons why a rapidly alternating spot might lose its motion quality faster than a slower one. It might provide a stronger signal which produced more adaptation during the induction phase, or it might provide a weaker signal which gave less visible motion during the test phase. Experiments in which we adapted to one alternation rate and tested on another showed that slow alternations (2.5 or 3 Hz) gave stronger motion signals than faster alternations (3.5 or 4 Hz).

Only motion could weaken apparent motion. The adapting spot had to traverse the same motion path as the test spot, and flicker alone produced little adaptation. If one adapted to two spots flickering in phase, and then tested on a single spot jumping back and forth, the motion percept was unimpaired. More surprisingly, an alternating dot had little adapting effect unless its motion was perceived along the adapting path. When the original

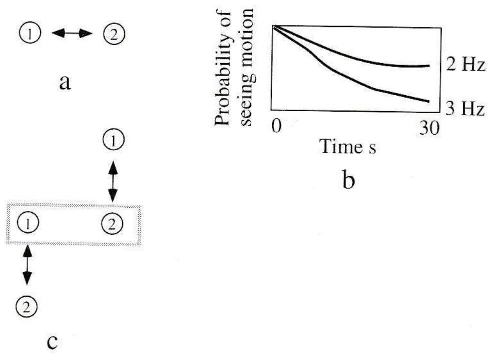

Fig. 4.2. a, A dot that alternates between two positions is first seen in apparent motion, but after a while the motion effect adapts out and the spots appear to flicker in place. b, Probability of seeing motion declines over time (Anstis *et al.*, 1985). c, Adaptation does not occur if the adapting and test dots have congruent positions but different perceived motion paths.

dot still flashed in alternation in the two usual positions, but two dots were added to the adapting display that caused two vertical motions to be seen with no perceived horizontal motion (Figure 4.2b), then again there was little adaptation.

4.2.3 Adaptation to random dynamic noise

Dynamic visual noise (DVN) is a snowstorm of randomly twinkling dots such as one can see on a detuned TV receiver. These dots jump around incoherently in apparent motion in random directions. Richard Gregory and I have found (in unpublished results) that adaptation to dynamic visual noise reduces motion sensitivity in all directions, like an omnidirectional motion aftereffect (Figure 4.3). Specifically, inspection of a twinkling field virtually halved the subjective speed of a subsequently viewed moving field. We measured this subjective slowdown by a matching method. Two adapting fields of dense random dots were presented side by side, a static field on the left and dots twinkling in random dynamic noise on the right. We used a 'topping-up' method in which the observers first adapted to this for 30 s, then alternately viewed this same adapting field for 4 s, alternating with 1 s views of a test field. The test field consisted of a random-dot field drifting downwards at 2.5° /s on the left, and a variable-speed drifting field, under the subject's control, on the right.

We found that following adaptation to the static dots the test velocity

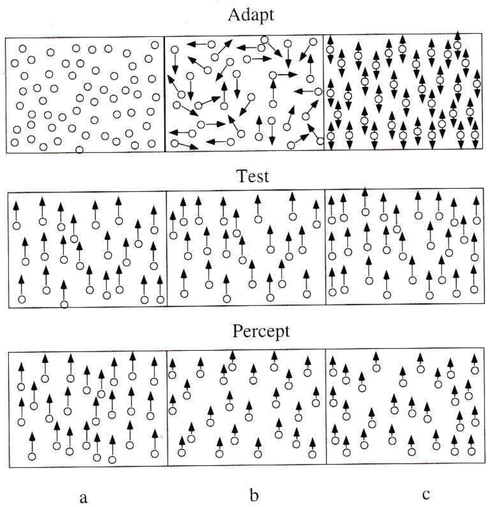

Fig. 4.3. a, Adaptation to a static noise field does not alter the perceived velocity of a drifting test field. b, Adaptation to a dynamic noise field slows it down, and so does c, adaptation to a random-dot field that moves up and down alternately.

was perceived accurately to within a few percent, as one would expect. However, adaptation to noise dramatically slowed the perceived test velocity (Figure 4.3b). Dots that drifted down at 2.5^o/s in the noise-adapted half of the field were matched to unadapted dots that drifted down at only 1.4^o/s – a 43% apparent slowdown.

4.2.4 Adaptation to opposed motions

Adaptation to downward motion generally makes a downward test motion look slower, because it unbalances the opponent-motion pathways that normally balance upward against downward motion (Sutherland, 1961; Sekuler & Levinson, 1974). Any stimulus that affects both opponent halves equally should cancel out and produce no motion aftereffect. This is so. Richard Gregory and I (unpublished results) adapted to dense random dots that moved alternately up and down at 2.5^o/s. We then looked for a motion aftereffect on a test field of dense random dots that was either stationary, or else drifted up [or down].

Adaptation to a field that moved back and forth produced no motion aftereffect on the stationary test pattern. This is not surprising, since the alternating motion clearly adapted upward and downward motion pathways equally, so the opponent motion detector would remain balanced and any equal but opposite motion aftereffects would cancel out. However, adaptation to the same alternating-motion field did produce a marked apparent slowing in a field of dense random dots that drifted up [or down]. (Figure 4.3c). We also observed apparent slowing during prolonged inspection of two superimposed sheets of random dots that drifted transparently over each other, one moving up, the other down.

The symmetrical adaptation from the double motion can produce this kind of asymmetrical aftereffect. Suppose that adaptation depressed the upward and downward gains to 80%. If the motion signals from a stationary test field were normally:

$$50U - 50D = 0 \qquad \text{(zero = stationary)}$$

then the double-motion adaptation would change this to:

$$40U - 40D = 0,$$

yielding no change in a stationary test field. If an upward moving test grating were normally signaled as:

$$100U - 10D = 90$$

then following adaptation its signal would be:

$$80U - 8D = 72$$

so the drifting grating would appear to be slowed down, as we found.

So this perceived reduction in following adaptation to up-and-down motion may be slowing down the perceived vertical test speed by reducing the strength of the motion signal. The Left/Right comparison model extracts motion from cells whose response can be altered in many other ways as well. Thus the Left cells could be firing because they saw something moving left or that it was the right spatial frequency or that it was the right orientation or high contrast etc. But the Right one would be affected by all those things too, so the comparison would bring out their only difference, direction. The absolute firing rates must be irrelevant here: it is only the Left/Right ratio that matters. Now adapting stimuli in which all directions get adapted would not affect the ratio. So it could not affect the comparison, that is, the motion information. If stimuli that affected all channels had an effect on velocity perception, then everything that affected all channels would have an effect, and high contrast patterns would appear to move faster. This has been demonstrated by Stone and Thompson (1992), who found that human speed perception is contrast dependent. They reported that when two parallel gratings moving at the same speed were presented simultaneously, the lower-contrast grating appeared slower. On average, a 70% contrast grating

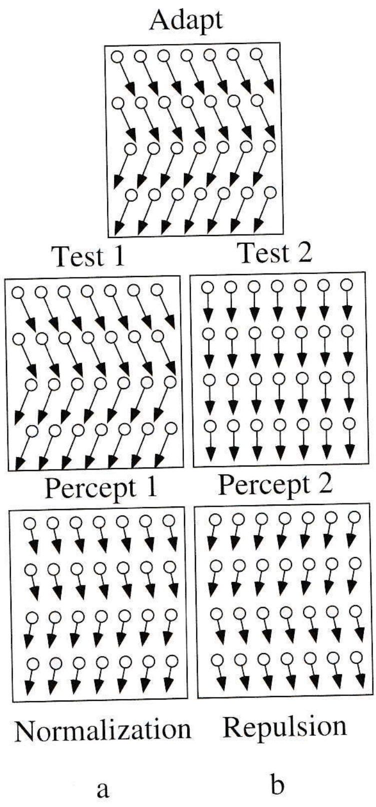

Fig. 4.4. An adapting field of sparse random dots moved downwards in a shallow V or chevron facing to the right. a, During prolonged inspection the dots appeared to slow down and their motion paths gradually shifted toward the vertical (motion normalization). b, a test field of dots that moved vertically appeared deviated into a motion path like a left-facing chevron (motion repulsion).

had to be be slowed by 35% to match a 10% contrast grating moving at 2^o/sec. The misperception of relative speed was reduced when the two gratings were presented sequentially. In their latest paper (Thompson *et al.*, 1996) they do greatly modify their conclusions but they do not abandon them.

4.2.5 Motion aftereffects of normalization and repulsion

I found it easy to confirm Marshak and Sekuler's directionally selective adaptation, in which adaptation to a downward motion toward 5 o'clock

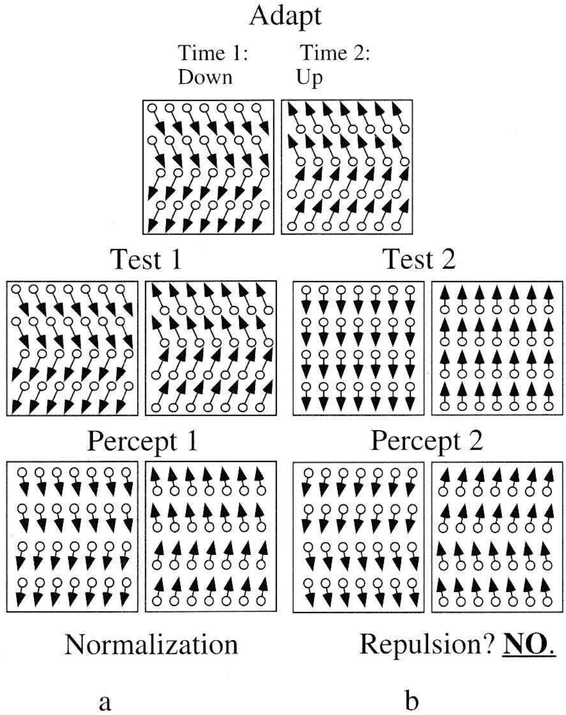

Fig. 4.5. As in Figure 4.4, except that the dots moved back and forth, reversing every 5 s. Result: some normalization occurred, but no repulsion aftereffect.

subjectively repelled a vertical test motion that drifts towards 6 o'clock by making it appear to drift toward 7 o'clock (Figure 4.4b). I used a field of sparse white dots on a black background drifting at 3^o/sec. The very same adapting field also produced an aftereffect of apparent normalization of motion. During the inspection period the random dots appeared to slow down markedly and in addition their trajectory seemed to shift gradually toward the vertical (Figure 4.4a). This is analogous to Gibson's (1937a, 1937b) discovery that a tilted line appears to regress toward the vertical during prolonged inspection.

Results were less clear cut when the adapting pattern reversed in direction every 5 s (Figure 4.5). The directions of adapting motion were approximately towards 11 o'clock and 5 o'clock, actually at 30^o from the vertical.

The direction alternated every 5 sec for a total adapting time of 10 minutes. The test field then moved alternately up and down vertically (toward 12 and 6 o'clock), reversing every 5 sec. Results: The moving dots still appeared to slow down during prolonged inspection, and they also normalized toward the vertical (Figure 4.5a). Following a 10 minute adapting period the observers viewed test dots that moved vertically up and down. Although these dots did appear somewhat slowed, their perceived motion paths were still correctly seen as vertical, with no angular deviation away from the vertical (Figure 4.5b).

4.2.6 Adaptation to expansion or to spatial-frequency change?

Adaptation to an expanding pattern yields a contracting motion aftereffect. Imagine a random-dot pattern, like a photograph of a sheet of sandpaper, which is electronically zoomed on a computer screen. After inspection of this pattern for about 30 s, a stationary test pattern will appear to be shrinking.

During the zoom, the contours that move outwards from the centre of the screen should suffice to stimulate motion sensors. But another way of looking at it is to say that the frequency spectrum of the pattern is zooming downwards. Since the Fourier transform that translates from space into spatial frequency is reversible in a linear system, both descriptions sound equally apt. Since we already know of visual pathways selective for gradual change of luminance (Anstis, 1967; Arnold & Anstis, 1993), Brian Rogers and I looked for hypothetical visual pathways that might respond to gradual change of spatial frequency. We attempted to adapt them by presenting a zooming display that lacked smoothly moving contours. Instead of zooming a static random-dot display, we zoomed a twinkling, dynamic random-dot noise display. This contained no smoothly moving contours but its frequency spectrum did zoom. Result: no motion aftereffect.

The spectrum of a random dot display is rather broad, so we narrowed it down with two sinusoidal gratings of the same spatial frequency (1 cpd). Both gratings expanded at the same rate (0.5 octaves/s), but whereas one simply expanded from its centre the other was jittered in phase, so that it translated randomly back and forth at right angles to its bars (Figure 4.6). Result: The smoothly expanding grating, which contained moving contours, did give a contracting motion aftereffect, but the jittered grating, which had a zooming spectrum but had no smoothly moving contours, showed no motion aftereffect.

Thus we were unable to find evidence for any phase-blind visual pathway that might be sensitive to gradual change of spatial frequency over time.

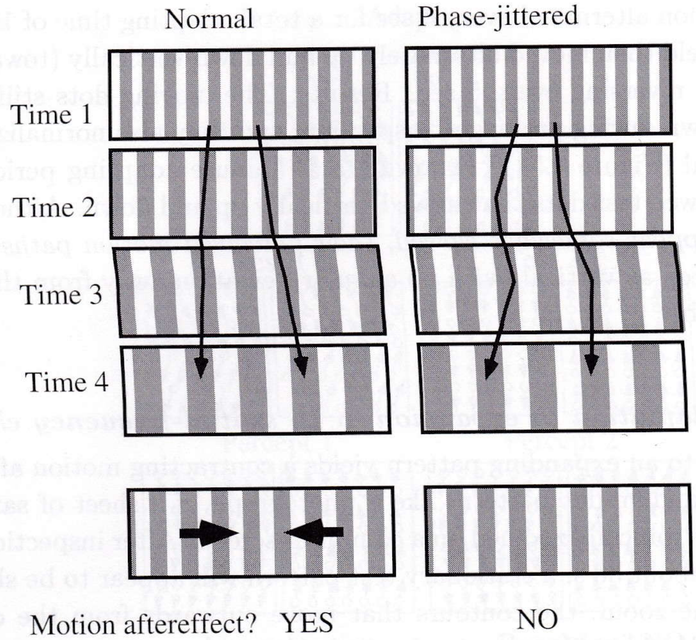

Fig. 4.6. An expanding grating gives a motion aftereffect of apparent contraction. However, a phase-jittered expanding grating does fall in spatial frequency over time, but it has no steadily moving contours, and it gives no motion aftereffect. Hence the aftereffect depends upon moving contours, not upon changes in spatial frequency.

4.3 Discussion

It is no accident that the visual system uses opponent pathways to code motion and colour. Opponency is widely used in electronic differential amplifiers, which receive two inputs and transmit only the difference between them. Respects in which the two inputs are the same are subtracted out and disappear. The higher the 'common mode rejection ratio' the better the amplifier.

All adaptation experiments are designed so that exposure to the adapting stimulus alters the appearance of the test stimulus. The test stimulus may become less visible, or may shift away from the adapting stimulus along some visual dimension (such as colour, motion, depth, etc.) A central assumption of all adaptation experiments is that such a change can only occur if the adapting and test patterns stimulate the same visual pathways. Therefore, if adaptation to motion makes a stationary pattern appear to move in the opposite direction, there must be some visual pathways that respond to both the moving and the stationary stimulus. This makes a clear physiological prediction that each opponent half of a motion detector must have a non-zero firing rate when confronted with stationary patterns. The firing rates are presumably identical in the two halves and cancel out exactly so that they do not appear at the output – any output signal would make stationary patterns appear to drift even in the absence of a motion aftereffect. A similar arrangement is known to exist for the semicircular canals (reviewed by Howard, 1982). Corresponding canals on each side of the head converge on an opponent pathway. Both canals have a resting output level, which cancel out. However, if one canal is destroyed or surgically removed, the remaining canal puts out a continuous unopposed resting level and the unfortunate patient feels the whole world constantly swimming around. The resulting vertigo is highly disabling and often there is nothing for it but to remove the other canal, a procedure which partially restores the status quo. The vertigo mercifully vanishes and the patient can maintain his balance reasonably well.

To summarize, all these results are consistent with the existence of opponent motion sensors, and they suggest several testable predictions. The sensors must contain temporal filters which respond to gradual change of luminance (+ dI/dT), and their velocity tuning curves must respond to stationary as well as to moving objects, such that the opponent halves, but not the final output path, produce a non-zero response to stationary stimuli. Adaptation to motion must reduce their gain rather than shift their zero point.

Acknowledgements Supported by NEI Grant EY 10241-4. Thanks to Laurence Harris and Dave Smith for comments on the manuscript.