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RECOVERING MOTION INFORMATION FROM LUMINANCE

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Abstract—We review evidence that visual transient channels responding to temporal change of luminance provide inputs to motion mechanisms, and also play a part in judgments of static brightness. These channels can be adapted to give aftereffects of apparent dimming or brightening. Nonlinearity in these channels causes a sawtooth grating to look dark (or light) while it is moving to the left (or right). The perceptual outcome in a competitive motion situation is governed by the larger temporal change in luminance: when a white bar and a black bar suddenly change places, on a dark (light) surround it is the white (black) bar that appears to move. The motion system responds to linear, not log luminance. If a black and white picture dissolves (fades) to its own photographic negative which if shifted a few min arc to the right "reversed apparent motion" is seen toward the left. These results constrain possible models of motion perception.

Motion perception   Apparent motion   Luminance   Contrast

INTRODUCTION

Consider a static visual display consisting of regions of different greys, blacks and whites. When a part or the whole of this display moves, some retinal receptors see brightening, others see dimming. How is this pattern of retinal luminance changes translated into a perception of movement? No single receptor on its own can see movement, so somehow the outputs of the retinal receptors must be compared to extract the motion signal. We shall present data which put constraints on possible models of the recovery of motion information from the retinal image. For instance, we can rule out models which discard luminance information in that they reduce the retinal image to a set of outlines, or which discard the sign (polarity) of luminance edges. However, our data do not discriminate between spatial and Fourier models of visual processing.

Luminance changes can take three forms: pattern, or spatial changes within a static retinal image with no temporal component: flicker, or temporal changes within a retinal image, with no particular spatial component: and motion, or spatio-temporal changes of the retinal image. We shall leave static patterns aside and consider only changing patterns, discussing visual responses first to temporal and then to spatio-temporal changes in luminance. We shall present evidence from adaptation experiments for the existence of "transient" visual channels which are selective to the direction (brightening or dimming) of gradual luminance change within a spatially uniform field. We shall show that these transient channels provide an input back to the perception of steady luminance, and forward to "motion-sensitive" channels which respond to the direction of movement.

ADAPTATION OF TRANSIENT CHANNELS WHICH RESPOND TO DIMMING OR BRIGHTENING

Following adaptation to a spatially uniform field which is growing gradually brighter, a subsequently viewed steady test field appears to be growing dimmer (Fig. 1). Conversely, following adaptation to a gradually dimming field, a steady test field appears to be growing brighter (Anstis, 1967). A convenient adapting field will ramp through a one log unit change of luminance in 1 sec of time and then repeat (Fig. 1). These two aftereffects probably result from selective adaptation of "transient" visual channels, of which some respond to gradual brightening, others to gradual dimming. The phenomena are minimal or absent if the changing field is too small, consisting of only a single pinpoint of light, or if it is too large, filling the entire visual field. A good stimulus is a field

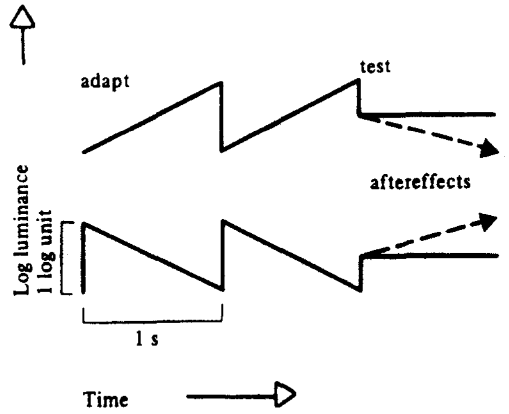

Fig. 1. After adaptation to a patch of light whose luminance was modulated with a series of slow, rising ramps, a steady test field (horizontal line) appeared to be growing gradually dimmer (dashed arrow). The aftereffect was a single downward drift in brightness, not a repetitive sawtooth. Conversely, after adaptation to a light which repetitively grew dimmer (lower sawtooth line), a steady test field appeared to be growing gradually brighter (lower dashed arrow) (Anstis, 1967).

about 1–10° across, centred in an unchanging grey surround which provides a reference brightness level. The aftereffects are localised to the stimulated region of the retina, since if the display is a checkerboard in which the white squares gradually turn black while the black squares are gradually turning white, aftereffects in appropriate directions can be seen simultaneously in the black and white squares of a steady test checkerboard. They are not artifacts of pupillary changes, since the mean luminance of the checkerboard display over time remains approximately constant over time; also the aftereffects are still observable through an artificial pupil. A single sweep of luminance is sufficient to generate the aftereffects, but in practice it is often convenient to modulate the adapting luminance with a repetitive temporal ramp or sawtooth, so that the log luminance gradually increases and then drops sharply. This gives rise to an aftereffect of apparent dimming. An adapting ramp which gradually dims and then sharply rises will produce an aftereffect of apparent brightening.

Information about gradual luminance change is probably an input for motion-sensitive channels. Marr and Ullman (1981) proposed a gradient model of motion detection which has two components: a spatial component which detects the polarity of an edge, and a temporal component which detects net dimming or brightening at the edge. Thus a light/dark edge produces net brightening when it moves to the right because the light region will now cover a previously dark region. The same edge produces net dimming when it moves to the left. Marr and Ullman's model (1981) specifically requires channels to measure the time derivative of the luminance signal, and the channels which adapt in response to gradual dimming or brightening are exactly what their model requires. Marr (1982) points out a critical empirical prediction from the model; if the temporal derivative input is abolished, the model either fails to respond at all, or, if it does respond, will lose its directional selectivity. It is not yet known whether this is true of directionally selective neural units in the visual system, but Moulden (1984) has tested and confirmed this prediction psychophysically by means of the dimming aftereffect. He pre-adapted his subjects to a spatially uniform, gradually brightening field, and found it raised their threshold for detecting a light/dark edge moving to the right. Adaptation to a dimming field raised the detection threshold for the same edge moving to the left. These results support Marr and Ullman's model. It must be admitted, however, that our findings are also consistent with Barlow and Levick's (1965) model of directional selectivity of neurons in the rabbit retina, provided that the sub-units of these neurons are themselves transient detectors.

So far as is known, no analogous aftereffects exist for colour. Several investigators have looked for such effects but not found them. F. W. Campbell (personal communication) superimposed a brightening red field on a dimming green field. This gave a spatially uniform field which gradually changed from green through yellow to red. However, no aftereffect of apparent colour change could be discerned on a steady yellow test field. D. M. Regan (personal communication) and B. P. Moulden (personal communication) have also adapted their subjects to a gradual sweep in wavelength along the spectrum, but did not find any aftereffect of apparent colour change in the opposite direction. This suggests that the neural site of the aftereffects cannot lie in the colour-opponent pathways, but must lie in the luminance channel, after the inputs from the red and green cones have been pooled (Fig. 2). It is intereresting to note that the colour channels do not seem to support motion perception either (Anstis, 1970; Ramachandran and Gregory, 1978).

It seems that the aftereffect depends on

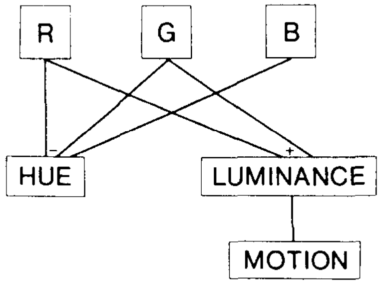

Fig. 2. Inputs from the red-, green- and blue-sensitive cones are combined subtractively via colour-opponent units to give hue, and inputs from red- and green-sensitive cones are combined additively to give luminance. Motion is probably mediated by the luminance channel, not by the chrominance (hue) channel.

perceived brightness rather than on luminance itself. Some factors, such as simultaneous contrast, which alter brightness without changing luminance, also alter the aftereffect. Consider a small grey spot of constant luminance which is centred in a spatially uniform surround which gradually changes from white to black. As a result of simultaneous contrast the spot appears to change gradually from black to white. If one now adapts to this display and then views a steady grey test spot centred in a steady grey surround, then the surround shows an aftereffect of apparent brightening, as one would expect. In addition, the spot shows an aftereffect of apparent dimming, even though its luminance has remained fixed throughout both the adapting and the test period (Fig. 3). Clearly the brightness of the spot, not its luminance, is implicated in the aftereffect. One might think that the apparent brightening which was spatially induced into the spot by the gradually dimming surround, sufficed to produce an aftereffect; this may be so, but there is a second possibility (Anstis, 1979). It might be that the aftereffect observed in the surround was spatially inducing a secondary aftereffect into the spot during the course of the adapting period itself. These two possibilities—an aftereffect produced by simultaneous contrast, and simultaneous contrast produced by an aftereffect—are shown diagrammatically in Fig. 4.

Anstis (1979), in a rather useless piece of puzzle-solving, devised two demonstrations which showed that both the effects exist and can be elicited independently. The first demonstration showed that aftereffects of apparent dim-

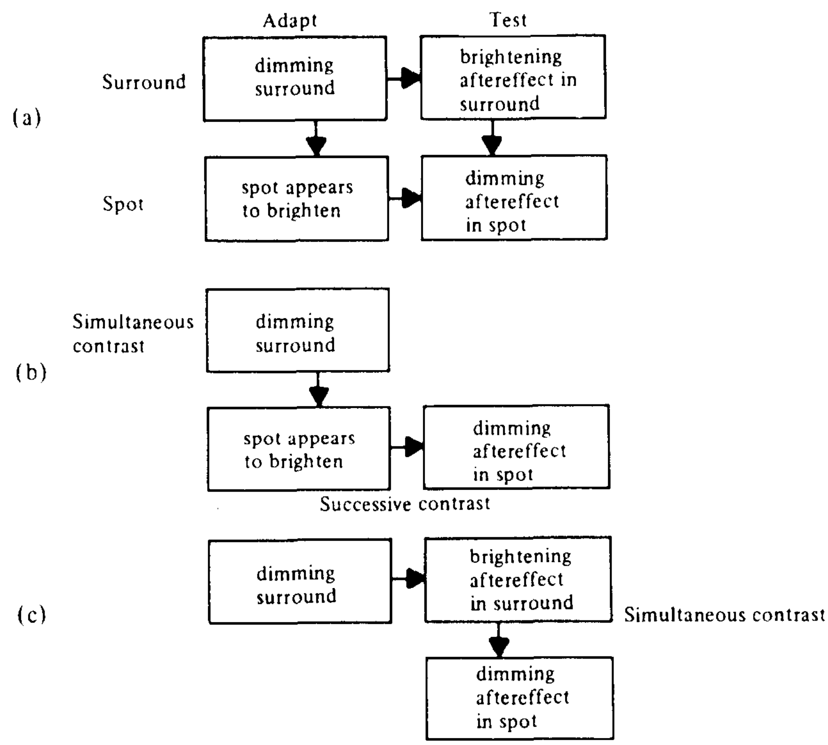

Fig. 4. (a) Two possible explanations of the aftereffects produced by contrast-induced brightness changes. (b) Aftereffect from contrast. The dimming of the surround made the central spot appear to be growing gradually brighter by simultaneous contrast, and this apparent change of the spot produced an aftereffect in the spot. (c) Contrast produced by a surround aftereffect. The gradual dimming of the adapting surround produced an aftereffect of brightening in the test surround, which then spatially induced a secondary aftereffect into the spot (Anstis, 1979).

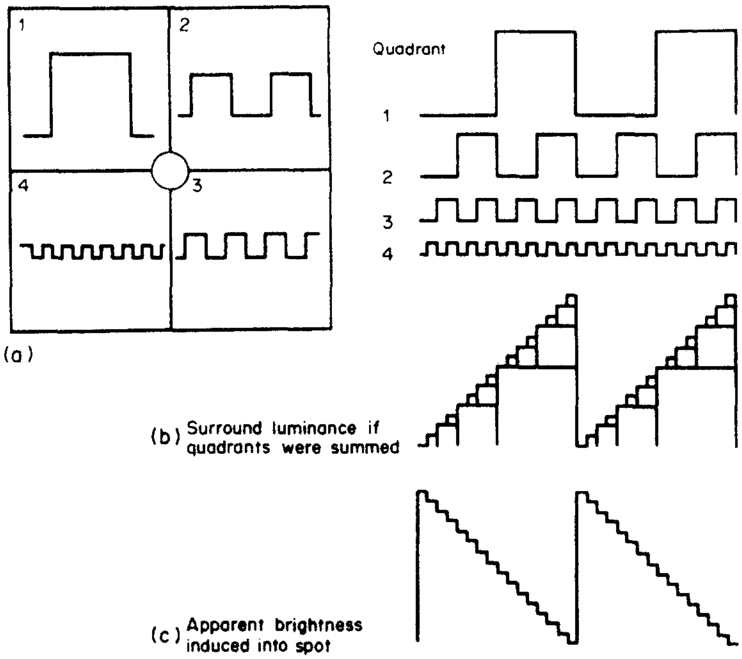

Fig. 5. (a) The surround was divided into four quadrants; each quadrant was modulated with independent but phase-locked temporal square-wave flicker. The flicker in quadrant 1 had a frequency of 1 Hz and a relative amplitude of 8; in quadrant 2, frequency 2 Hz and amplitude 4; in quadrant 3, frequency 4 Hz and amplitude 2; and in quadrant 4, frequency 8 Hz and an amplitude of 1. These quadrants were carefully kept spatially separate, but if they had been superimposed they would have summed to a rising ramp (b). In fact, each quadrant spatially induced an upside-down version of its own flicker into the central spot by simultaneous contrast. Thus, these induced flickers summed up to a falling ramp (c). Result: following adaptation, the spot showed an aftereffect of apparent brightening, in the absence of any possible surround aftereffect (Anstis, 1979).

ming or brightening in an adapting spot could be caused by neural processes taking place during the adapting period. This was done by carefully excluding any aftereffects in the test surround. The adapting surround was divided into four quadrants, each of which was independently modulated in luminance over time by means of a separate, but time-locked square wave, such that each quadrant varied with twice the frequency but half the amplitude of its neighbour (Fig. 5). Quadrant No. 1 was made to flicker at a frequency f and a relative amplitude which we shall arbitrarily call 8: quadrant No. 2 flickered at frequency $2f$ and relative amplitude 4: quadrant No. 3 at frequency $4f$ and amplitude 2: and quadrant No. 4 at frequency $4f$ and amplitude 1. If these four flickering quadrants had been spatially superimposed, which they deliberately were not, then the four square waves would have summed together to produce a digitally synthesised staircase which approximates to a rising temporal luminance ramp. (It is quite a good approximation, containing all the Fourier components of a ramp except for the sixteenth harmonic and multiples thereof.) It was arranged that the inner corner of each quadrant abutted on the small central spot, and spatially induced into this spot an "upside-down" version of its own waveform. These four upside-down waveforms were spatially summated within the small (1 deg) spot to produce a falling temporal brightness ramp. Thus the brightness of the spot appeared to fall gradually, then jump sharply up again. Adaptation to this sufficed to produce a small aftereffect of apparent brightening in a steady test spot. Note that this was produced purely by the apparent brightness change which was spatially induced into the spot during the adapting period. By design, there was no aftereffect in the surround because the square-wave flickers in the quadrants of the adapting surround were symmetrical with respect to time and contained no ramp-like components of net dimming or brightening. So the aftereffect in the test spot was not induced into the test spot by the (nonexistent) aftereffects in the surround during the test period.

The second demonstration had the opposite intention, and showed that an aftereffect in the

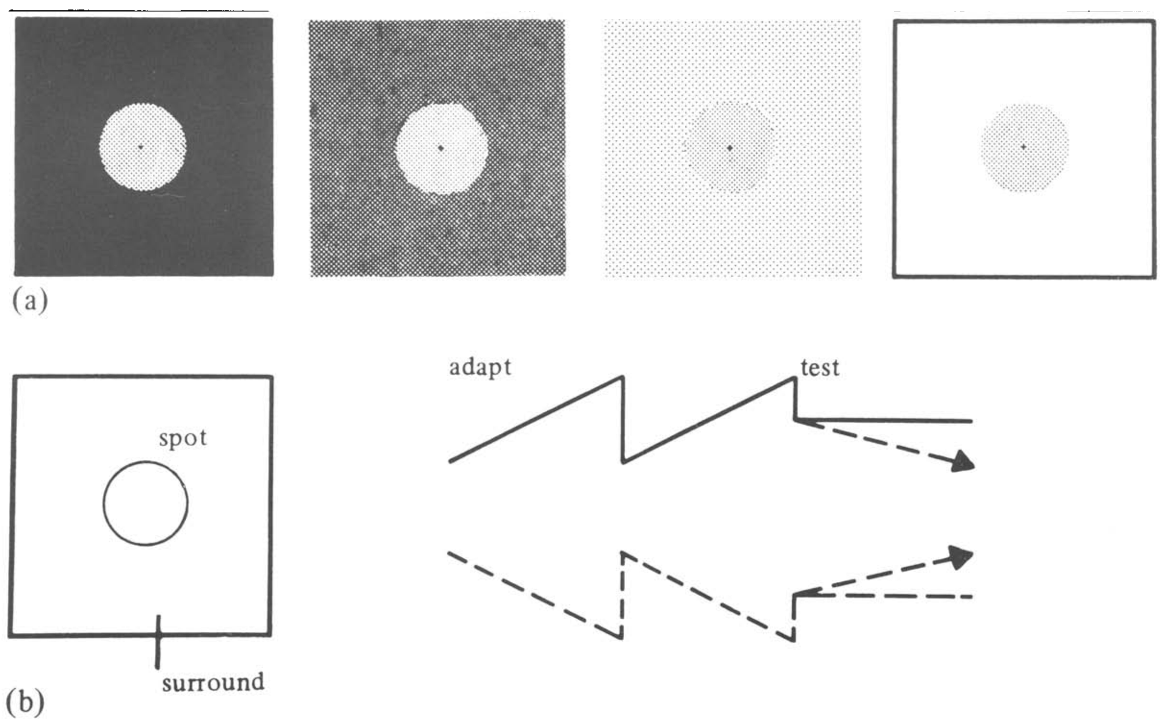

Fig. 3. (a) Diagram of the surround luminance at four instants during a sweep or ramp from dark to light. All four central spots have the same physical grey in this illustration, but simultaneous contrast made the spot appear to be gradually dimming as the surround brightened, and vice versa. (b) When the adapting surround gradually brightened (upper sawtooth, solid line) and then switched to a steady luminance (upper horizontal, solid line) it showed an aftereffect of apparent dimming during the test period (upper dashed arrow). The spot appeared to dim during the adaptation period (lower sawtooth), and then gave an aftereffect of apparent brightening (lower dashed arrow), even though its physical luminance had remained fixed at all times (Anstis, 1979).

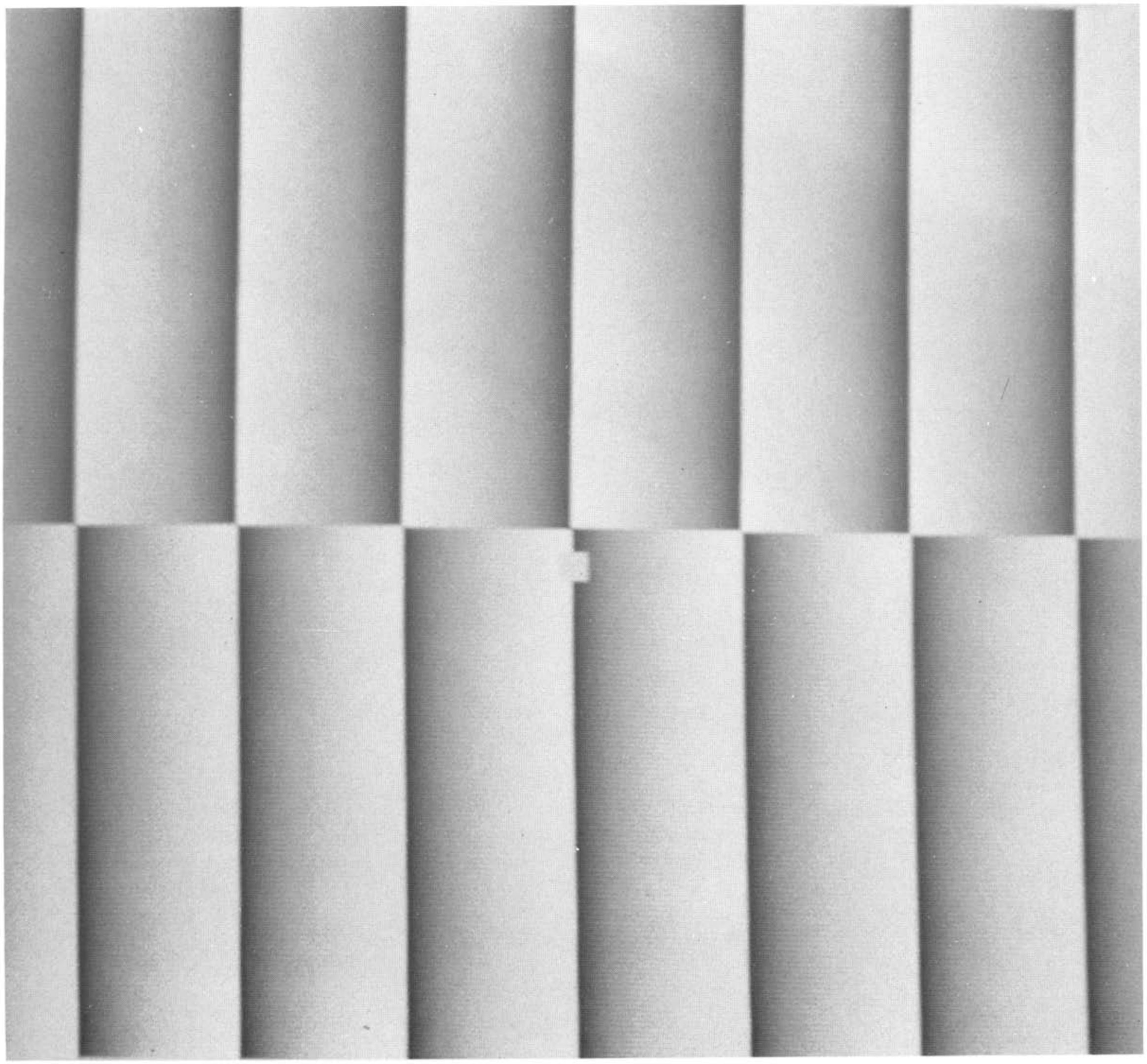

Fig. 7. Two gratings of shaded bars with sawtooth luminance profiles. If the eyes follow a fixation point which moves to the right along the line separating them, the upper grating appears darker than the lower grating.

surround could spatially induce an aftereffect into a test spot. The adapting display consisted of a grey spot of constant luminance centred in a surround which was an annular 1 log unit wedge filter disc (Fig. 6). This disc was rotated clockwise for 30 sec and then stopped. Note that during rotation (and adaptation) any static point in the surround was scanned by the wedge filter, so that its luminance was modulated by a repetitive rising ramp. Examples are shown for some arbitrary surround points in Fig. 6. However, the rising ramps did not spatially induce any brightness change into the centre spot, since by symmetry the rotation produced no net change in the spot's surround. After a period of rotation the disc was stopped, and a strong aftereffect of apparent dimming was seen in the surround. In addition, an aftereffect of apparent brightening was seen in the spot. This could not be produced by (nonexistent) apparent dimming in the adapting spot, but must have been spatially induced by the surround aftereffect during the course of the test period.

We conclude from these studies that:

1. "Transient" visual channels exist which are selective for the temporal derivative of luminance, that is, for the direction of gradual luminance change over time. Some channels respond to brightening, others to dimming and these channels can be adapted separately.

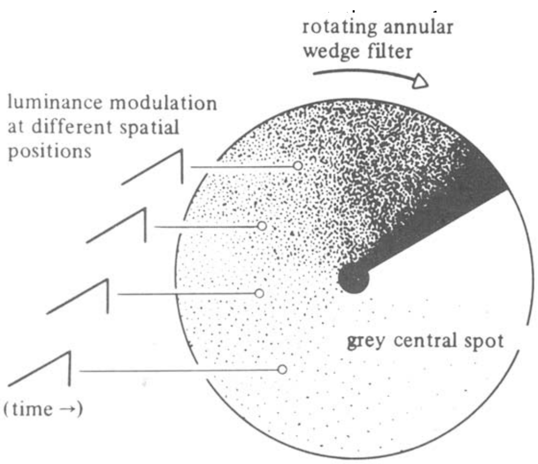

Fig. 6. The adapting field was a central grey spot of fixed luminance, centred in a rotating annular wedge filter. Any stationary point seen through the rotating filter repetitively grew gradually brighter, so when the motor was stopped, all parts of the filter showed a pronounced dimming aftereffect. This spatially induced an aftereffect of brightening into the spot. Notice that the adapting spot did not appear to be dimming during the rotation, because the rotation did not alter the net luminance over time of the surround (Anstis, 1979).

2. These channels are part of the luminance system, not the chrominance (hue or opponent-colour) system.

3. The existence of the induced aftereffects of gradual luminance change show that these channels lie central to the site at which lateral inhibition or simultaneous contrast operate.

4. These transient channels provide inputs to channels that respond to motion.

In the next section we shall show that the output of these transient channels is used in judgments of steady luminance level.

MOVING SPATIAL RAMPS OF LUMINANCE

A grating with a ramp or sawtooth luminance profile consists of shaded bars. Figure 7 comprises two such gratings. The bars of the upper grating are shaded from light to dark and of the lower grating from dark to light. Run the point of a pen along the horizontal border between the two gratings and track it with the eyes. Patrick Cavanagh and I noticed that when the fixation point moved to the left (right) the upper grating looked lighter (darker) than the bottom grating. The time-varying sawtooth change from the stimulus puts it up on an illusory "pedestal" of brightness.

The effect is not determined by the Fourier power spectrum of the two stimuli, which are mirror images and so share the same Fourier components, differing only in spatial phase. Instead it relates to the slope of the luminance profiles. We have investigated two possible explanations for the effect. Except at the edges of the bars, a small leftward movement of the upper grating reduces the luminance on a given retinal patch: thus a light-adapted retinal region receives a slightly dimmer stimulus. This will tend to make the grating look dimmer. Conversely a retinal region inspecting the lower grating will be dark-adapted and receive a brighter stimulus, so the lower grating will look bright. By analogy, if one adapts to an upper white patch and a lower black patch and then views two identical grey patches, the upper grey patch will look dimmer than the lower one. We can call this the "static light-adaptation" hypothesis.

A more interesting hypothesis is that when the upper grating moves steadily to the left it generates a repetitively dimming temporal ramp which stimulates the dimming detectors described in the previous section. The lower grating stimulates brightening detectors. Moreover the second-order signal from these dynamic detectors is integrated and added into the first-order steady-state signal from static luminance detectors. We can call this the "dynamic light-adaptation" hypothesis.

The spatial ramps consist of a gradual upward slope and a sharp return. Both ramps in Fig. 7 have the same mean luminance, so the fact that one looks brighter than the other suggests a nonlinear sensing of luminance. We suspect that the brightening or dimming detectors show a nonlinear saturation and fail to respond fully to a very rapid slope. This is akin to "slew rate limiting" in amplifiers. We are still investigating these effects (Cavanagh and Anstis, in press).

CROSSOVER MOTION

Mather and Anstis (1985) have found that luminance can determine the direction of apparent motion in an ambiguous display. We presented two parallel horizontal bars, a white bar above a black bar, on a grey surround. Suddenly the two bars changed places, so now the upper bar was black and the lower bar was white. In other words the upper bar changed from white to black and at the same instant the lower bar changed from black to white (Fig. 8). Does this stimulus look like a white bar jumping downwards, or a black bar jumping upwards? We found that the direction of apparent motion was determined by the luminance of the surround. On a light grey surround it was the black bar, and on a dark grey surround it was the white bar, that was seen as jumping. So the bar that differed more from the surround (i.e. that had the higher contrast) was seen as moving. On a mid-grey surround, when the two bars had the same luminance contrast, they both seemed to jump in opposite directions simultaneously. Except at or near this mid-grey, only one of the bars was seen as moving. The other bar was seen as a stationary object alternately covered and uncovered by a jumping bar (Sigman and Rock, 1974). Thus the visual system segregated the dynamic display into an apparently moving "figure" and an apparently stationary "ground".

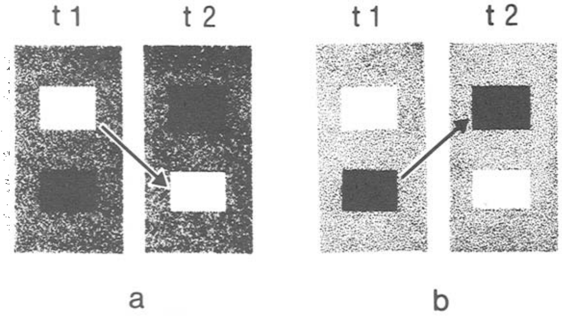

Fig. 8. A black and white bar changed places. (a) On a dark surround a white bar was seen jumping downwards. (b) On a light surround a dark bar was seen jumping upwards (Anstis and Mather, 1985).

We called this mid-grey the "indifference luminance" and measured its value when the black and white bars were selected from a palette of six luminances ranging from 3.2 to 160 cd/m^2. We found that the indifference luminance lay at the arithmetic mean, exactly halfway between the luminance of the black and white bars. It did not lie at the geometric mean. This implies that the motion mechanism responds to linear not log luminance; that is, the strength of signal that it gives in a competing motion situation depends on the difference of linear luminance at the moving edge. This is surprising because many published studies show that the visual system imposes a log transform on luminance inputs, as exemplified in the Weber–Fechner law (equal ratios of luminance produced equal differences in response). It is also surprising that linearity held up over such a wide range of luminance and contrast, in view of Keck *et al.* (1976) finding that the motion system saturates at quite low levels of contrast. We cannot explain these discrepancies.

The separation between the bars was not critical, since apparent motion could be seen when the bars were separated by 1 or 2°, and also when they were touching. Timing was also not critical; instead of the bars being switched between black and white they could be made to fade gradually over a second or so, with the dark bar becoming lighter while the light bar was becoming darker, and a gliding apparent motion could be seen. The direction of apparent motion alternated back and forth as the two bars alternated in luminance, as one would expect, but by modifying the display we were able to produce continuous apparent motion in one direction. The bars were touching, and were modulated over time by counterphase triangular waves, so that one bar gradually grew lighter as the other grew darker. At the end of each fade the surround was made to switch in luminance between light and dark (Fig. 9). First, on a dark surround, the upper light bar grew dimmer as the lower dark bar grew brighter. Observers reported a light bar gliding downwards. At the

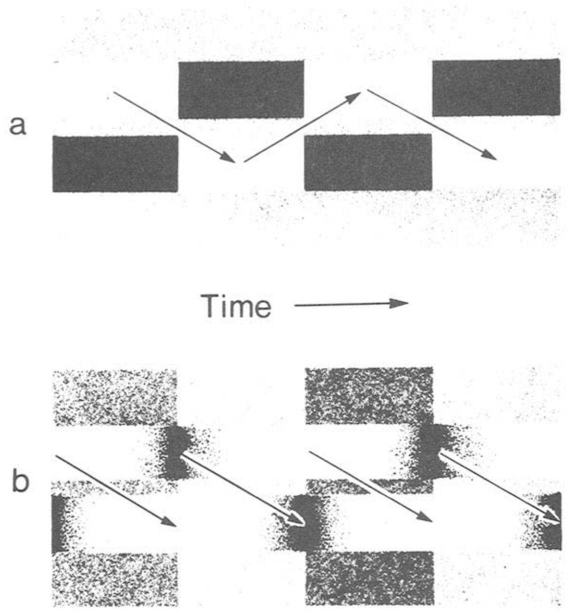

Fig. 9. (a) A replot of Fig. 8(a) over several successive cycles. (b) A modified version of Fig. 8 which gave a strong impression of continuous downward motion. The luminances of the upper and lower bars were modulated over time by counterphase triangular waves, so one bar gradually grew lighter as the other grew darker. At the same time, the surround luminance was modulated by a square wave so that it switched from light to dark or vice versa at each peak of the triangular wave: this square wave was phased in time so that it produced unidirectional apparent motion of a white bar apparently moving down, then a black bar moving down. The cycle repeated endlessly (Anstis and Mather, 1985).

end of the fade the surround was switched to a high luminance. The bars now faded back to the other way, with the initially dark upper bar growing brighter and the initially light lower bar growing darker. Since the surround was bright, motion of a dark bar was now reported. This motion was also downwards. So the apparent motion was now always downwards, although the moving bar was alternately light and dark. The percept of unidirectional motion was extremely robust; although hard to describe on paper it was compelling when viewed on videotape, and observers found it hard to believe that the bars were not actually drifting across the screen. If the stimulus cycled repetitively it could generate a strong upward aftereffect of motion. This strongly suggests that the display was stimulating neural motion detectors. Incidentally, the apparent motion would go upwards instead of downwards if the relative timing of the luminance changes in the surround and the bars was reversed.

These experiments showed that when luminance changes in the surround signalled two opposed potential movements, it was the movement with the higher contrast that predominated. The stimulus is reminiscent of a counterphase flickering grating, which is equivalent to a pair of superimposed gratings moving in opposite directions. If the two gratings have the same contrast an observer sees motionless flicker, but if the contrast of the leftward (or rightward) moving grating is raised then motion is seen to the left (or right) (Sekuler and Levinson, 1974). We have stated that the motion system responds to linear, not log luminance, so it is interesting to note that the Michelson contrast of a grating $[(L_{max} - L_{min})/(L_{max} - L_{min})]$ is also defined in terms of linear, not log luminances.

These results are consistent with an opponent model of directional selectivity (Reichardt, 1961), in which motions in opposite directions are subtracted and the stronger motion signal predominates. Although our data fit this model they do not compel us to accept it; but they do show the importance of luminance and contrast in directional selectivity.

REVERSED APPARENT MOTION FROM REVERSED LUMINANCE CONTRAST

A black and white pattern which makes a small, sudden jump to the right will be perceived in apparent motion to the right. This can conveniently be done by putting two slides of the same pattern into two projectors, projecting the two images on to the same screen in overlap but with a small displacement, and exposing first one image then the other, like a movie which is only two frames long. Instead of cutting or switching suddenly between pictures, one can dissolve between pictures, that is, fade one picture down and at the same time fade the other picture up, keeping the total luminous flux on the screen roughly constant. This changed timing still gives apparent motion to the right, but the pattern now seems to glide instead of jump [Fig. 10(a)].

Suppose the jumping pattern is a square wave grating. Is its apparent motion best described in spatial terms as a set of black or white areas which suddenly shift, or in Fourier terms as a set of spatial frequencies, each of which can be considered independently? It is well known that a square wave is composed of a set of odd harmonics or Fourier components with spatial frequencies f, $3f$, $5f$, $7f$, $9f$. . . . Let us suppose that the grating jumps through one-quarter of a spatial cycle to the right. It follows that the fundamental also jumps through one-quarter cycle, but the 3rd, 5th and 7th harmonics jump through respectively three-quarters, five-quarters and seven-quarters of a spatial cycle. The third harmonic's jump of three-quarters of a cycle to the right is equivalent to one-quarter cycle to the left, and the fifth and seventh harmonics also jump one-quarter cycle, effectively to the right and left respectively. Thus for any sized jump of the whole grating the different harmonics will effectively jump in different directions, some in the same direction as the fundamental, others in the opposite direction. It is counter-intuitive to suppose that the visual system responds separately to the independent motion of each harmonic, each moving through a different phase angle, and then somehow puts all these different motions together again. However, Adelson (1982) has devised a neat demonstration that this may be what happens. A square wave grating which jumped in successive quarter-cycle steps to the right was seen as jumping to the right; but when the fundamental component of the square wave was removed the direction of apparent motion reversed and was now to the left, determined by the leftward jumps of the third harmonic. (Since the harmonics have lower amplitudes than the fundamental, their apparent motions are presumably masked as a rule by that of the fundamental.)

Now suppose that the second pattern in our two-frame movie is the photographic negative of the first. Something surprising happens; during the dissolve from one to the other, the apparent motion is now seen to the left, in the opposite direction to the image displacement [Fig. 10(b)]. We have called this effect "reversed apparent motion" (Anstis, 1970; Anstis and Rogers, 1975; Rogers and Anstis, 1975). The pattern can be a grating, or random blobs, or anything, and it makes no difference whether the positive or the negative pattern comes first, in fact with random patterns it is arbitrary which is called the positive and which the negative. The timing is not critical, since any fade duration between about 0.5 and 5 sec will give the effect, and the apparent motion is seen continuously during all stages of the fade. However, the spacing is critical, and the displacement between the two patterns must not exceed about 6–10 min arc in foveal viewing (Anstis and Rogers, 1975). This is comparable to Braddick's (1974) spatial limit of 15 min arc, which is the maximum distance across which short-range apparent motion can be seen.

To understand this effect let us consider it first in the Fourier and then in the spatial domain. Consider a simple sinusoidal grating which jumps to the right, say through one-tenth of a spatial cycle, and reverses in contrast as it does so. The contrast reversal is equivalent to a jump of half a cycle, so the combination of reversing it and shifting it by 0.1 cycles to the right is equivalent to shifting it by 0.4 cycles to the left. Not surprisingly, it will be seen jumping to the left. If a square wave grating is used (instead of a sine wave) its Fourier fundamental will still jump through 0.4 cycles to the left, and thus give reversed apparent motion. However, its spatial harmonics will shift variously to the left and right, depending on the jump size. Why do these moving harmonics not mask or disrupt the reversed apparent motion carried by the fundamental? There are two possibilities. Either the amplitudes of the harmonics are too low for them to make much difference, or else they are actually attenuated by spatial filtering or neural blurring in the visual system. Evidence drawn from the spatial domain suggests that neural blurring does occur. In our model (Anstis and Rogers, 1975; Rogers and Anstis, 1975), the shifted negative is superimposed on the positive during a slow fade, and the composite positive–negative contours are neurally blurred by a Mexican hat function. This filtering rounds off the contours into S-shaped luminance profiles which shift progressively to the left during the fade [Fig. 10(b)]. On this model the upper harmonics, which have lower amplitudes in the stimulus, are further attenuated by the visual system. Gregory and Heard (1983) have made extensive measurements of reversed apparent movement and related phenomena.

We conclude that luminance information is crucial to the motion system, since contrast reversal can lead to apparent motion reversal. Reversed apparent motion is compatible both with a spatial and with a Fourier account, but any worthwhile model of motion perception must be able to explain it. For instance Marr and Ullman (1981) point out that their gradient model of directional selectivity can account for reversed apparent motion.

CONCLUSIONS

We have traced just a few of the steps by which luminance information is translated into

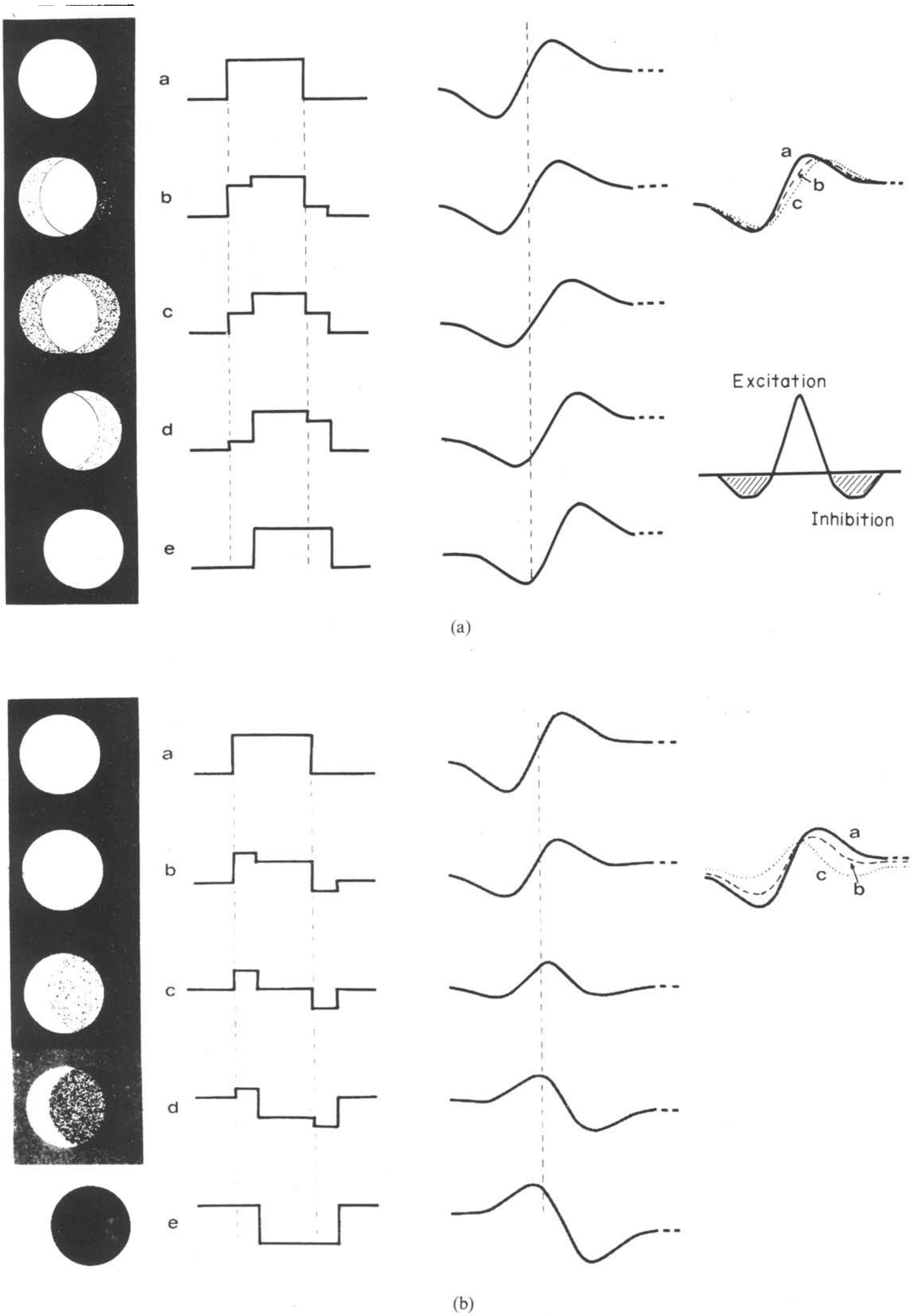

Fig. 10. (a) When a black and white pattern fades via a dissolve to a copy of itself which is displaced to the right, gliding apparent motion is seen to the right. First column: the stimulus at times (a–e). Second column: luminance profile of the stimulus. Third column: result of convolving the left-hand edge of this luminance profile with the Mexican hat operator shown at bottom right. Top right: these convolved profiles at times (a), (b), (c) are superimposed to show steady displacement of the stimulus to the right. (b) When the second pattern is the photographic negative of the first, then reversed apparent motion is seen to the left, opposite to the direction of physical displacement. On right: the convolved profiles at times, a, b, c are superimposed to show steady displacement to the left (Anstis and Rogers, 1975).

the perception of motion. There are visual transient channels that respond to the temporal derivative of luminance, that is to gradual brightening or dimming, and their existence was demonstrated by adaptation which led to aftereffects of apparent dimming or brightening (Anstis, 1967). These fit nicely into Marr and Ullman's (1981) model, which requires that brightening and dimming signals be available to the motion channels, and Moulden's cross-adaptation experiment (1984), in which adaptation to brightening or dimming reduced the sensitivity to a moving edge of appropriate luminance polarity, shows that these signals come from the transient channels. We conclude that these transient channels provide inputs to the motion processes. From our experiment on moving spatial ramps we conclude that the signals from the transient channels are also fed back as a component of judgments of static brightness.

A competitive, crossover motion stimulus was used to explore the role of luminance changes in signalling motion. The amplitude of luminance change was important. In our experiments on crossover motion a white bar suddenly became black and a black bar became white. This gave good apparent motion, and measurements over a wide range of luminances revealed that the input to motion consists of linear, not log, luminance. Our results showed that when luminance changes in the stimulus signalled two opposed potential movements, it was the motion with the higher contrast that predominated.

Our experiments on reversed apparent motion showed that edge polarity information was preserved by the motion system. This fits the models of both Reichardt (1961) and Marr and Ullman (1981). Adelson (1982) suggested that apparent motion was signalled by the Fourier components of a square wave grating, not by its edges; our studies of reversed apparent motion did not resolve this issue, but they indicated that the motion system neurally blurs the stimulus contours or, what amounts to the same thing, responds primarily to low spatial frequency components and perhaps filters out higher frequency components altogether.

We cannot claim that our experiments rule out any of the existing models of directional selectivity proposed by Reichardt (1961), Barlow and Levick (1965) or Marr and Ullman (1981). All we can say is that our results impose constraints that future models will have to satisfy. The keen current interest in motion perception indicates that such models will not be long in appearing.

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