PERGAMON

Vision Research 40 (2000) 657–675

Vision Research

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Luminance processing in apparent motion, Vernier offset and stereoscopic depth☆

Stuart M. Anstis [a], David R.R. Smith [a b,*], George Mather [b]

[a] *Department of Psychology, University of California San Diego, La Jolla, CA 92093, USA*
[b] *Department of Experimental Psychology, School of Biological Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK*

Received 6 July 1998; received in revised form 8 February 1999

Abstract

We obtained (apparently) linear responses to luminance from three special displays of apparent motion, Vernier offset and stereoscopic depth. In our motion stimulus a dark and a light bar exchanged luminances repetitively on a grey surround. Motion was attributed to the bar that differed more from the surround, that is, on a dark surround the light bar appeared to jump, and on a light surround the dark bar appeared to jump. The apparent motion disappeared when the luminance of the surround lay halfway between that of the bars — on a linear, not a logarithmic scale. Similar results were obtained for special Vernier offset and stereo stimuli. These results cannot be explained if all luminances are processed within the same luminance pathway *and* that pathway transforms input luminance using non-linear compression. However, the apparent linearity of our results could arise from opposite and equal non-linearities cancelling out within separate ON- and OFF-spatial luminance pathways. A second set of experiments presented one bar separately into each eye on different surrounds (dichoptic presentation of competing apparent motion signals) or manipulated the display spatially so that different surrounds were associated with different bars (binocular presentation of competing Vernier targets). Results showed that apparent motion and Vernier signals of equal Weber contrast (normalisation of linear difference to surround luminance) evoked equal-motion and equal Vernier offset strengths. Given that motion and Vernier strength followed Weber's law, we infer that the ON- and OFF-pathways transform luminance non-linearly. Our third experiment presents an example of a brightness bisection task in which we were able to influence the bisection steps, to follow either a linear or non-linear series. The benefits of parsing the visual scene so that visual information is processed within two opposite luminance pathways is discussed. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Brightness; Weber contrast; Apparent motion; Stereopsis; Vernier acuity; ON- and OFF-pathways; Scaling

1. Introduction

In our everyday life we typically move around in and operate fairly comfortably (i.e. see quite well), in an enormously wide variety of light levels ranging over some ten log units, which is approximately the difference between starlight and the midday sun. Given the limited dynamic range of the retinal photoreceptors (the rods and cones have an operating range of around three and two log units, respectively, Baylor, Nunn & Schnapf, 1984, 1987), there is a huge discrepancy between the wide range of possible light levels incident upon the photoreceptors and the far narrower range of available responses to those light levels (Uttal, 1973; Walraven, Enroth-Cugell, Hood, Macleod & Schnapf, 1990). The visual system needs to solve/address this input–output bottleneck problem otherwise it is threatened with the loss of valuable visual information.

The visual system, through evolutionary pressure, has developed several strategies to ameliorate potential information loss at the input–output bottleneck. One important process is multiplicative adaptation where the operating range of the sensory system goes up or down to match the mean light level thus discounting

☆ Parts of this work were originally presented in May 1997 and May 1998 (Smith, Anstis & Mather, 1997; Anstis, Smith & Mather, 1998a) at the Association for Research in Vision and Ophthalmology Annual Conference in Fort Lauderdale, FL, USA, and at the 1998 European Conference on Visual Perception in Oxford (Anstis, Smith & Mather, 1998b).

* Corresponding author. Fax: +44-1273-678611.
E-mail address: dsmith@biols.susx.ac.uk (D.R.R. Smith)

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PII: S0042-6989(99)00205-9

the illuminant (von Helmholtz, 1867; Craik, 1940). We are unaware of this constant tracking of mean light levels by the visual system unless we move rapidly between two very different light levels, such as say a very dark room and the sunny outside, when we find ourselves briefly dazzled by the strong light. Another way the visual system can circumvent the input–output bottleneck is by compressive response non-linearities. One such non-linearity is logarithmic compression, an idea dating back to at least the mid-nineteenth century when it was first explicitly stated by Fechner (Fechner, 1860).

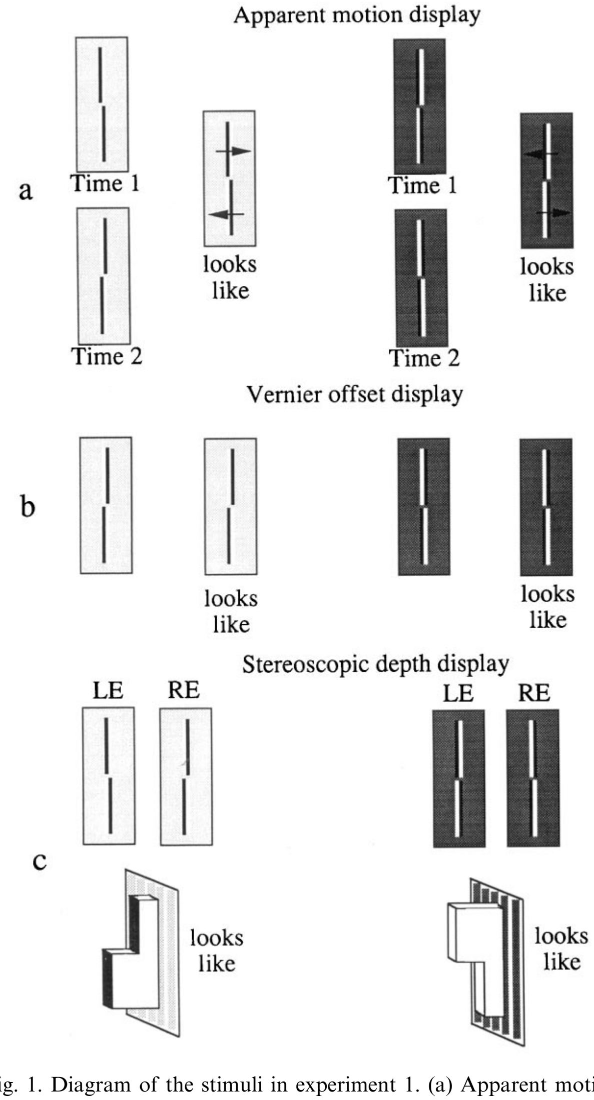

Fig. 1. Diagram of the stimuli in experiment 1. (a) Apparent motion display. Two frames alternated in the apparent motion task, with the luminances of the stimuli exchanging on a constant grey surround. On a light surround the dark bars appeared to move. On a dark surround the light bars appeared to move. (b) The Vernier offset display. When a top light–dark Vernier target was placed above a bottom dark–light Vernier target then the percept was determined by the grey of the surround. (c) The stereoscopic depth discrimination task. LE and RE denote the left and right eye percepts, respectively. The depth percept was determined by the grey of the surround.

Fechner argued that the sensation of luminance is proportional not to stimulus luminance but to the log of that luminance. There is strong empirical evidence for this (reviewed in Poulton, 1989). This is clearly shown by the setting of equal interval brightness scales (Munsell, Sloan & Godlove, 1933; Whittle, 1992). In one typical demonstration an observer is shown a set of n panels, of which the leftmost panel is black and the rightmost panel is white. The observer is invited to adjust the luminance of each of the in-between panels until s/he is satisfied that the panels form steps of equal-brightness (brightness being our subjective perception of luminous intensity). Invariably the observer sets the panel luminances L_j so that the ratio between each pair of panel luminances (L_j/L_{j+1}), not the difference $(L_j - L_{j+1})$, is equal. These equal-ratio settings define a logarithmic series. For instance, if we let the black panel be 1 and the white panel be 100 in arbitrary units, then observers set the in-between panel luminances $(n = 5)$ to approximately 3, 10 and 32. Taking the logs of the elements of the series 1, 3, 10, 32, 100 we find that each number is an equal difference from the other on a logarithmic scale. Such a series is compressive because a greater difference in physical luminance is required at the high end than at the low end, to produce the same subjective amount of change in brightness. Whittle's (1992) observers set equal subjective interval scales consistent with brightness being a function of the log of panel luminance L_j except when L_j was near the luminance of the surround L_S upon which the panels were superimposed. When L_j was near to the surround luminance then brightness was a function of the log of $\Delta L_j (= |L_j - L_S|)$. This area of enhanced luminance discrimination near to surround luminance (cf. Whittle, 1986), is called the 'Crispening Effect' after Takasaki (1966). See Gilchrist (1994) for a detailed discussion.

In this paper we examine the nature of the visual response to luminance in three visual tasks: apparent motion, Vernier offset and stereoscopic depth discrimination. Does the visual system rescale input luminance by passing stimulus luminance through some kind of transform (e.g. a logarithmic function), or does the visual system operate upon raw stimulus luminance (linear function)? The connection between brightness perception and these three spatial tasks, which are concerned with retinal position rather than with levels of luminance, may not be immediately obvious. And indeed there would be no connection if the targets used were simply white lines on a black surround (or vice versa). In this study we bring grey scale into the picture by superimposing two apparent motions, or Vernier offsets, or stereo depths, which are of different contrasts and in opposite spatial directions, upon backgrounds of various luminances. For instance, Fig. 1(a) shows an apparent motion stimulus adapted from Anstis and Mather (1985). A dark bar and a light bar , side by side and touching, suddenly exchange places. What does an observer see? Does s/he report a dark bar jumping to the right, a light bar jumping to the left, or both of these at once? Or simply two bars which flicker in place? It turns out that the answer depends upon the luminance of the surround. On a light surround, the dark bar appears to jump, and on a dark surround, the light bar appears to jump. The bar which differs most from the surround is the one seen as moving.

At some surround luminance there occurs a null point where neither bar dominates. We term this null point the 'indifference luminance point', i.e. the surround luminance against which the sensations generated by the light and dark bars are equal and opposite, so that no net motion (or Vernier offset, or stereo) is seen. The luminance value of this indifference point should tell us how the visual system treats the luminances of the two bars. Specifically, if the bar luminances are processed in a linear fashion then the indifference point should occur at the arithmetic mean of the two bar luminances. This implies that at equal luminance *differences* from the surround the two bars generate equal strengths of sensation. However, if equal strengths of sensation require that the two bars have equal-ratio*s* against the surround then the indifference luminance point should occur at the geometric mean, which in turn would imply that the luminances of the two bars are equidistant from the surround on a logarithmic scale. Briefly, if the indifference point is at the arithmetic mean then this suggests that input luminance is processed linearly, and if the indifference point is at the geometric mean then it suggests a logarithmic transformation is applied to input luminance. In this paper we measure the indifference luminance point for apparent motion, Vernier offset and stereoscopic depth discrimination.

This paper describes three main experiments. First, we examine three vision tasks (apparent motion, Vernier offset and stereoscopic depth discrimination) in which the visual system seems to operate upon input luminance linearly. Our first set of experiments was performed with binocular presentation. Our second set of experiments examines the rôle of Weber contrast in apparent motion and Vernier acuity, using dichoptic and binocular presentation, respectively. Finally, we show how a brightness bisection task where the visual system seems to transform luminance logarithmically at high contrasts but linearly at low contrasts, can be manipulated so that the visual system seems to transform luminance linearly for all contrasts.

2. Experiment 1

2.1. Methods

The stimuli, examples of which are shown in Fig. 1, were generated on an Amiga 4000 computer (Anstis, 1986; Anstis & Paradiso, 1989) and viewed in a darkened room from a distance of 57 cm. The vertical line stimuli were 1.8° long by 3.4 min (1 pixel) wide. Line stimuli were presented as upper and lower line pairs of opposite polarity. The upper and lower line pairs were separated by a vertical gap of 0.2°. Each upper and lower line pair consisted of two contiguous vertical lines. Expressing luminances as a percentage, where white (100%) was equal to 64.5 cd/m^2, the line luminances were selected as a pair from the set: 0, 3, 13.5, 34, 65 and 100% (= 0, 2, 8.7, 22.1, 42.1 and 64.5 cpd/m^2). Line pairs were presented on a uniform grey surround 5.6° high by 1.9° wide. There were 24 grey surround panels (arranged in a 3×8 matrix) varying in luminance from 0 (black) to 64.5 cd/m^2 (white) in 4% steps. Each panel was surrounded by a black border 0.8° high by 0.4° wide.

Observers selected the panel on which the effects were minimal (cf. task descriptions below). For the apparent motion task this was when neither dark nor light bar motion dominated the percept, for the Vernier task when the upper and lower line pairs seemed to be aligned, and for the stereoscopic depth discrimination task when the upper and lower line pairs seemed to lie in the same depth plane. Eight subjects took part in this experiment.

2.1.1. The apparent motion task

The upper and lower line pairs consisted of dark–light and light–dark pairs, respectively, exchanging their luminances over time at the rate of 1 Hz (i.e. the upper line pair was dark–light for 500 ms, then light–dark for 500 ms, and so on). Thus the potential apparent motions of the dark and the light line were pitted against each other (cf. Anstis & Mather, 1985). Whether the observers reported apparent motion of the dark or the light line was determined by the luminance of the surround (Fig. 1a).

2.1.2. The Vernier task

A standard Vernier target typically consists of vertical lines, either dark lines on a light background or light lines on a dark surround. The observer's task is to state whether the upper line is displaced to the left or right of the lower line. Vernier acuity is extraordinarily good with a just discriminable threshold of around 5 sec arc, well below the diameter of a retinal cone (Westheimer, 1979). It makes little difference to performance whether the display is dark-on-light or light-on-dark. In this paper we combined the two, always using decidedly suprathreshold Vernier displacements. The Vernier target consisted of a pair of lines, light–dark in the upper half and dark–light in the lower half, on a grey surround. The upper and lower line pairs were exactly aligned. This stimulus can be thought of as a light Vernier target, with the upper line displaced 3.4 min to the left, superimposed on a dark Vernier target, with the upper line displaced 3.4 min to the right. Which of these two opposed stimuli dominates, the dark or the light? It turns out that this also depends upon the luminance of the surround (Fig. 1b).

2.1.3. The stereoscopic depth discrimination task

We also studied a stereoscopic version of the Vernier target. The left eye was shown one Vernier stimulus as just described, whilst the right eye was shown its mirror image, reversed from left to right. The luminance of the surround determined whether the light or the dark lines predominated. When the dark lines predominated observers saw the upper dark line in uncrossed disparity so that the upper line appeared to be further away than the lower line. When the light line lines predominated observers saw the upper light line in crossed disparity so that the upper line appeared to be nearer than the lower line (Fig. 1c). In the stereo displays the stimuli to the left eye and to the right eye were drawn on alternate TV fields and viewed through special liquid-crystal flickering goggles. This gave excellent stereo depth with minimum cross-talk between the eyes but it unavoidably reduced the luminance seen by each eye by approximately 1.5 log units (a factor of 30).

In summary, our experiments measured the indifference luminance of the surround, defined as the particular grey level for which the perceptual effects were minimal. We made separate measurements for the motion, Vernier and stereoscopic depth discrimination tasks.

1. At some intermediate surround luminance, observers saw ambiguous apparent motion. They reported either that the motion went away, or that the light and dark lines appeared to jump simultaneously in opposite directions.
2. At some intermediate surround luminance, observers saw an ambiguous Vernier offset. The upper line did not reliably look either to the left or the right of the lower line.
3. At some intermediate surround luminance, observers saw ambiguous depth. The upper line did not reliably look either nearer or farther away than the lower line.

These percepts were measured whilst varying three luminance levels: those of the left line, the right line, and the surround. By using many different combinations of left and right line luminances we built up data into a three-dimensional surface. We can compare this empirical surface to the theoretical surfaces predicted by linear or logarithmic transforms of input luminance.

2.2. Results

Fig. 2 shows our data as a set of three-dimensional plots, where the x-axis gives the left bar luminance (cd/m^2), the y-axis gives the right bar luminance and the z-axis gives the indifference luminance of the surround (the point at which the percept was ambiguous). Data are plotted separately for apparent motion (Fig. 2a, b) Vernier offset (Fig. 2c, d) and stereoscopic depth discrimination (Fig. 2e, f). Conventions are the same for each graph. The linear hypothesis predicts the surround indifference luminance should be at the arithmetic mean of the two bar luminances. In other words, the surround indifference luminance z would be equal to $(x+y)/2$. This hypothetical surface is plotted in Fig. 2(a, c, e). It is equivalent to the plane surface that is freshly exposed when one cuts along the grand diagonal of a cube. If the visual system responds linearly to input luminance in the experiments then the data points should lie on this surface, within the limits of experimental error. On the other hand, if the visual system applied a logarithmic transform to input luminance then the data would lie on the convex-upwards curved surface $\sqrt{(x \cdot y)}$ (Fig. 2b, d, f). The error distances, represented by the height at which each datum point floats above or below the hypothetical surface, indicate how well our data fit the linear and logarithmic hypotheses. The smaller the error scores, the better the fit. (For clarity, the perpendicular dropped from each datum point to the surface is drawn with a small horizontal foot resting on the surface.)

The data bear upon two main questions. First, are the observed data more consistent with a luminance response based on a linear transform, or on a logarithmic transform of the input luminance? Second, do the apparent motion, Vernier and stereoscopic depth discrimination tasks all give similar results? If so this suggests a common underlying pathway.

Casual inspection of Fig. 2 shows larger errors (longer vertical lines) for the log surfaces than for the linear surfaces. This impression is amply confirmed by statistical analyses. We compared the fit of our experimental data with the linear and logarithmic predictions by calculating the mean of the squared errors of prediction:

$$\sum_{i=1}^{n} (z_i - z'_i)^2/n \qquad (1)$$

where z'_i is the model prediction (either linear or logarithmic), z_i is the observed indifference luminance point, i is each combination of right and left bar luminances, and n is the number of paired observations in the experiment. The smaller these error scores, the better the data fit the model.

The results were: 10.26 (apparent motion against linear) and 67.54 (apparent motion against logarith-

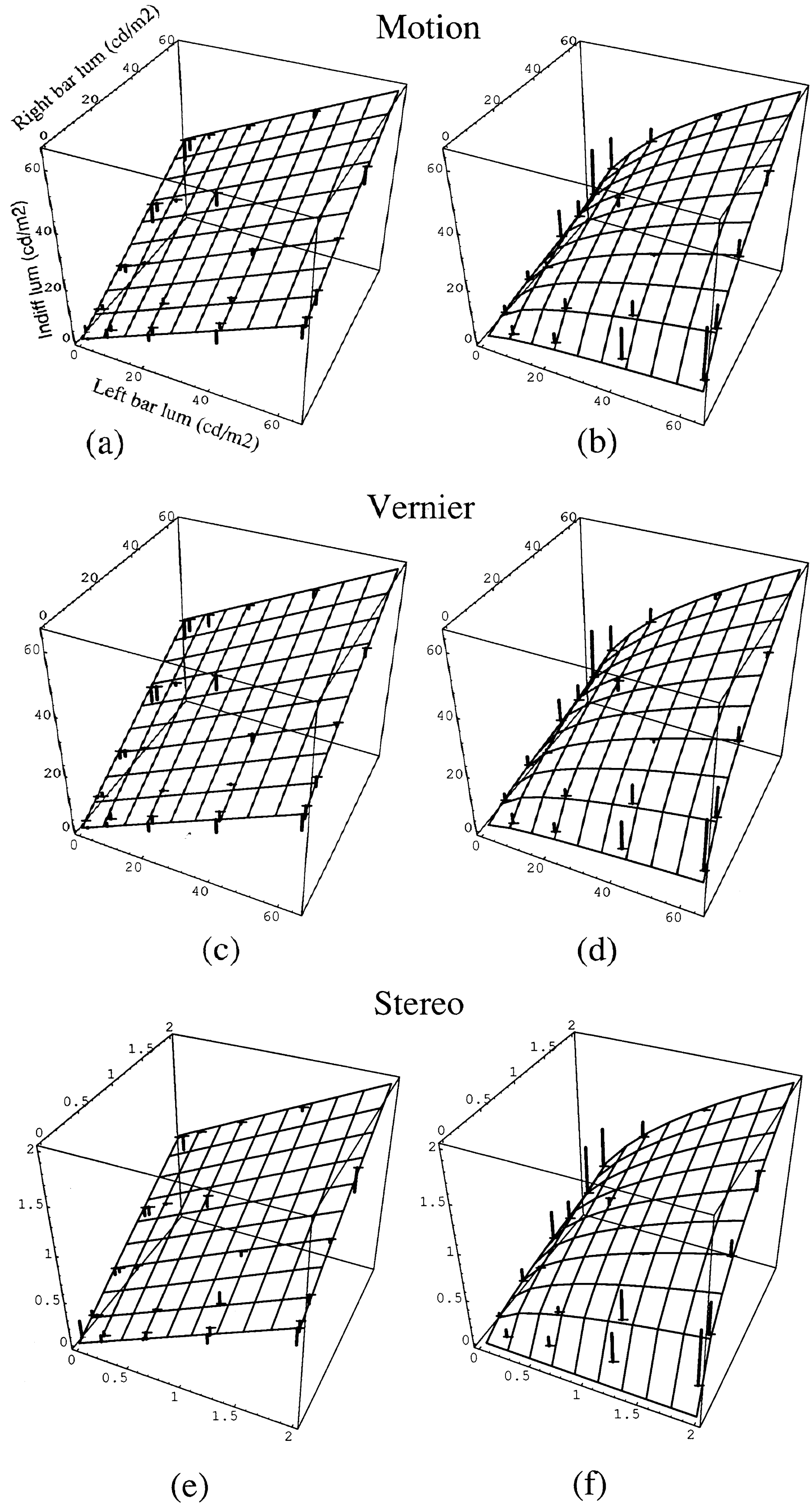

Fig. 2. Results for experiment 1. The indifference luminance of the surround (z-axis) as a function of left (x-axis) and right (y-axis) bar luminance (all measured in cpd/m^2). Vertical lines, representing error distance, connect each data point to the value predicted by a linear or logarithmic model (the mesh plane). For clarity each error line has a little horizontal foot resting on the mesh surface. (a, b) Apparent motion task. (c, d) Vernier discrimination task. (e, f) Stereoscopic depth discrimination task.

mic); 9.86 and 59.96 (Vernier against linear and logarithmic, respectively); and 8.7 and 70.55 (stereoscopic depth discrimination against linear and logarithmic, respectively). The liquid-crystal flickering goggles used to produce stereo reduced the luminance seen by each eye by approximately 1.5 log units. The luminance range (and hence the size of the error scores) was therefore effectively scaled down by a factor of 30 (unscaled values were 0.0087 and 0.0707 for stereoscopic depth discrimination against linear and logarithmic predictions, respectively). To correct for this reduction we multiplied each observed error score for the stereoscopic depth discrimination condition by 1.5 log units before squaring and summing. This makes comparison between the stereoscopic depth discrimination condition, and the motion and Vernier tasks easier. Clearly the error scores were at least six times greater for the log than the linear predictions. We applied the F-ratio test to all our data. Two-sided P-values were less than 0.001. The experimental data are a better fit to the linear than the logarithmic model across all three conditions.

We also fitted a popular non-linearity (gradual saturation to asymptotic level) of neural response, the Naka–Rushton (Michaelis–Menten) model (e.g. Naka & Rushton, 1966) to our data, using the equation:

$$R = \frac{L}{L + L_s} R_{max} \quad (2)$$

where R is response, L is stimulus luminance, L_s is the semi-saturation constant (the luminance giving half the maximum response), and R_{max} is the luminance giving maximum response. We let R_{max} be the highest bar luminance we used, which also provides L_s.

The mean of the squared errors of prediction were: 27.27 (motion against Naka–Rushton); 23.56 (Vernier) and 37.63 (stereoscopic depth discrimination). Therefore the Naka–Rushton fit was better than logarithmic (smaller errors) but still worse than the linear case. For reasons detailed below, we felt it unnecessary to test the fit of other candidate functions.

Our results suggest that the depth, hyperacuity and motion systems all operate linearly upon luminance. This is a very surprising result given the evidence for logarithmic compression from other psychophysical studies (Poulton, 1989; Whittle, 1992), as well as the physiological evidence, e.g. the logarithmic-like relationship between rod and cone amplitude response peak and photon density (Schnapf & Baylor, 1987), and the nature of the threshold-vs.-intensity changes in gain of single rods (Baylor et al., 1984).

Certainly our data are inconsistent with a logarithmic scaling of response anchored at some near-zero luminance because the luminance values of the stimuli (x and y) and the surround (z) do not lie equidistant from each other on a logarithmic scale. This is to say the luminances x, y and z cannot be processed by the *same* pathway if that pathway transforms input luminance logarithmically. However, there is a way of explaining our data using a logarithmic response scale if we think more about the particular nature of our experimental setup. Notice that the surround, at the null point, always lies exactly halfway between the luminances of the two stimuli and this necessarily means that one stimulus has a luminance value less than the surround while the other stimulus has a value greater than the surround. One stimulus is thus an incremental (or ON) signal while the other is a decremental (or OFF) signal. Therefore the two stimuli are qualitatively different (rather than just quantitatively different) and such different stimuli could be processed by separate pathways. The existence of separate parallel pathways in the brain specialized for the processing of ON- or OFF-signals is well-known (Kuffler, 1953; Schiller, 1982, 1984; reviewed in Schiller, 1992). Furthermore, as the surround lies halfway between the two stimuli, the ON-signal input strength is potentially the same as the OFF-signal input strength.

Now it is perfectly possible that the ON- and OFF-pathways logarithmically compress their inputs (indeed they might have any kind of non-linearity including none, i.e. be linear!). However, if the nature of the luminance transform is the same in each pathway, *and* both pathways have the same magnitude of input *and* the response of each pathway is subtracted from the other then the result would be *apparent* linearity of the system. The linear behaviour of our experiments might be the consequence *of equal and opposite non-linearities cancelling each other out*. When our observers are deciding when the two potential motions (or Vernier offsets or stereo depths) are equal, the observer might first parse the display into separate ON- and OFF-signals, and then proceed to balance the signal strengths within each sign sensitive luminance pathway by choosing a surround luminance that gives equal luminance difference (ΔI) between each stimulus and the surround ($=I$). With our current experimental setup where both stimuli are seen against the *same* surround luminance, equal and opposite non-linearities will cancel out at the arithmetic mean (assuming approximate symmetry of gain in the ON- and OFF-pathways). Within this interpretation of our data, the common surround provides the same reference point from which to measure the activity within each separate pathway. The common surround provides a zeroing point or normalisation level (or more loosely, a frame of reference within which to interpret the relative strength of the signal). Moreover, if this parsing into ON- and OFF-signals does occur then we are left with no knowledge of the nature of the processing being applied to input luminance within each separate pathway.

We need an experiment where each stimulus is presented on a different surround. This will allow us to determine whether the results from our first set of experiments demonstrate linear processing of luminance in a common pathway (sign of luminance is disregarded — only magnitude of luminance is important) so that luminance difference ΔI determines equality of competing luminance signals; or whether the data in our first set of experiments can be explained as signals with equal but opposite sign Weber fractions ($\Delta I/I$) cancelling out. In the latter case, the pattern of results in our second set of experiments (different stimuli on different surrounds) should help us to decide what kind of non-linearity, if any, operates within each signed luminance pathway. We concentrated on our apparent motion and Vernier offset tasks when exploring this issue.

3. Experiment 2

The deficiency of our first set of experiments, where both stimuli were presented on the same surround, was remedied in experiment 2 by arranging for each stimulus to lie on a different surround. We did this with a dichoptic display which presented (say) a white bar on a light grey surround to the left eye, and (say) a black bar on a dark grey surround to the right eye. The two bars jumped back and forth in counterphase, and were fused binocularly to give a display equivalent to a black and a white bar exchanging luminances on a grey surround. This dichoptic display was perceptually equivalent to the binocular display used in experiment 1. The advantage was, however, that we could now discover whether bars of equal-motion strength each differed by a constant absolute luminance from their respective surrounds:

$$(L_{\mathrm{Bar}}^{\mathrm{LE}} - L_{\mathrm{Surr}}^{\mathrm{LE}}) = (L_{\mathrm{Bar}}^{\mathrm{RE}} - L_{\mathrm{Surr}}^{\mathrm{RE}}) \quad (3)$$

or whether each bar luminance was normalised with respect to its respective surround:

$$\left(\frac{L_{\mathrm{Bar}}^{\mathrm{LE}} - L_{\mathrm{Surr}}^{\mathrm{LE}}}{L_{\mathrm{Surr}}^{\mathrm{LE}}}\right) = \left(\frac{L_{\mathrm{Bar}}^{\mathrm{RE}} - L_{\mathrm{Surr}}^{\mathrm{RE}}}{L_{\mathrm{Surr}}^{\mathrm{RE}}}\right) \quad (4)$$

This last equation predicts that *bars with equal Weber fractions (i.e. possessing the same Weber contrast), will have equal-motion strengths whatever the absolute values of their surrounds*. If one presupposes that any given motion strength (as defined by its Weber fraction), is made up of motion strength 'units', and that these units are subjectively equivalent regardless of the normalising luminance of the surround, then results in accordance with Eq. (4) would be consistent with a logarithmic scaling of stimulus luminance (we use the same integration argument as Fechner (1860) applied to Weber's Law for differential sensitivity). In other words, if motion strength k is equal to $(L_{\mathrm{Bar}}^{\mathrm{LE}} - L_{\mathrm{Surr}}^{\mathrm{LE}}/L_{\mathrm{Surr}}^{\mathrm{LE}})$, it is also equal to $\log(L_{\mathrm{Bar}}^{\mathrm{LE}} - L_{\mathrm{Surr}}^{\mathrm{LE}}) - \log(L_{\mathrm{Surr}}^{\mathrm{LE}})$.

For each pair of bars, experiment 1 provided only one datum point for a single null point lying at the mean of the bar luminances. Experiment 2 extended the data from a single point to a complete curve, by using two surround luminances which were presented one to each eye and pitted against each other. Whereas experiment 1 involved three luminances (bar 1, bar 2, surround), our dichoptic display gave us four (bar 1, bar 2, surround 1, surround 2) which gives us an extra degree of freedom to play with. When the two pictures were fused binocularly, the dark bar signal from one eye was compared with the light bar signal from the other eye, and presumably the stronger motion signal would predominate. Indifference would occur when these light bar and dark bar motion signals were of equal strength. In our previous experiments we could measure this only when both signals were of equal strength against the same surround luminance, but this constraint is now removed.

3.1. Methods

The views for the left eye and right eye were displayed side by side on a monitor screen, and fused binocularly by means of base-out prisms near the eyes, together with a septum in the sagittal plane. Stimuli were generated on an Amiga 4000 computer (Anstis, 1986; Anstis & Paradiso, 1989), and viewed in a darkened room from a viewing distance of 57 cm. Two subjects (the first and second authors) took part in this experiment.

Fig. 3(a) shows examples of the stimuli. Two horizontal bars exchanged positions at an alternation rate of 1.25 Hz, each bar being 1.64° wide × 0.44° high and separated by a gap of 0.26°. Each bar was located in a uniform grey surround 3.75° wide × 2.9° high, which in turn was centred in a field of dense black and white random dots, 6.2° wide × 5.5° high. These dots, which were identical to both eyes, were provided as an aid to binocular fusion. Whereas in experiment 1 both eyes had seen both bars on a common surround, in this experiment the left eye saw one bar on one surround and the right eye saw the other bar on a different surround. Typically the bars and the surrounds seen by each eye differed in luminance. For each run, the left eye's stimulus was preset to one of several different combinations of bar and surround luminance thus creating incremental and decremental bar stimuli of Weber contrast ±16, ±20, ±40, ±84 and ±100% (bar to surround luminance (bar:surround) of 70:84, 100:84, 50:84, 92:50 and 100:50, respectively, in percentages where 100% (white) was equal to 67.6 cd/m^2). On each trial the right eye's bar was preset to different values, and the observer adjusted the luminance of the right

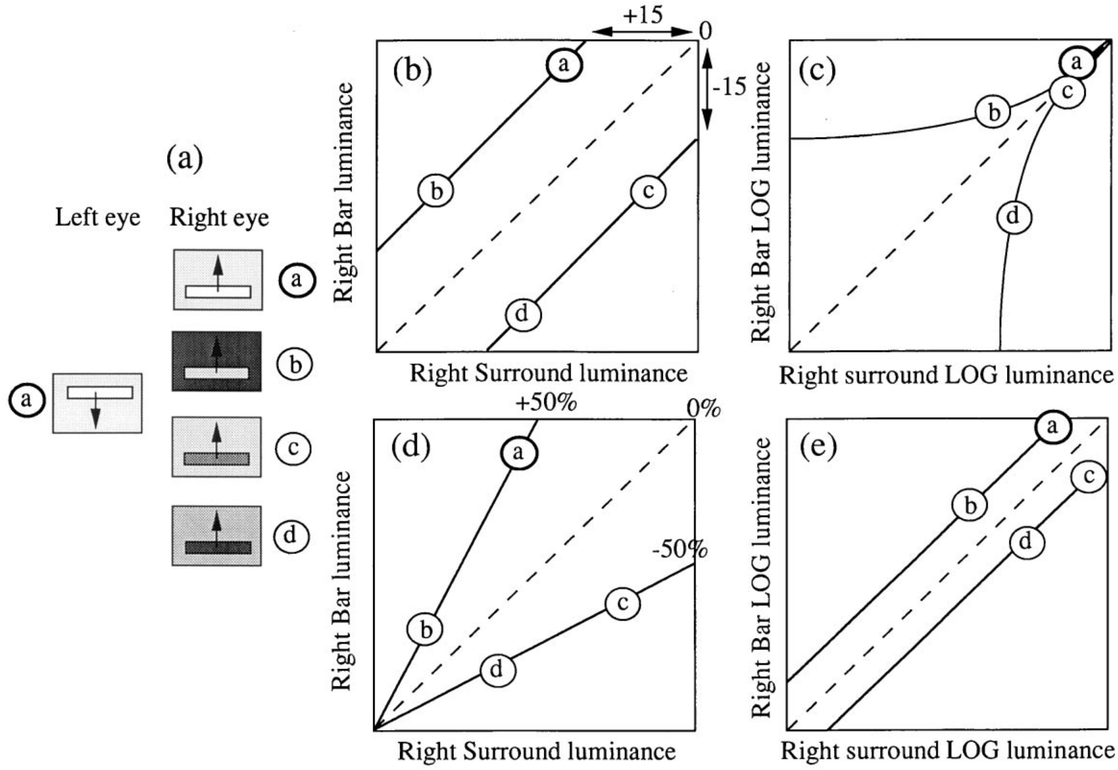

Fig. 3. Diagram of stimuli and *hypothetical* results for experiment 2. (a) In the dichoptic display of experiment 2, the left eye always saw the same bar, say a spatial increment jumping downwards. The views of the two eyes were fused binocularly. The experiment consisted of finding a set of right eye bars, both increments (a, b) and decrements (c, d) whose upward motion just cancelled out the left eye's downward motion. (b–e) Lines connect data points which had the same motion strength. If a *strict linear* relationship holds then we would expect the pattern of results shown in (b) and (c) when plotted on double-linear and double-log co-ordinates, respectively. If a *Weber contrast* relationship holds (a linear difference that is normalised with respect to each eye's surround), then we would expect the pattern of results shown in (d) and (e) when plotted on double-linear and double-log co-ordinates, respectively.

eye's surround by pressing two keys which increased or decreased the luminance in steps of 4%, until he or she was satisfied that the motion of neither bar predominated. This defined the indifference luminance point. Observers matched each left eye combination of bar and surround luminances to both spatial increments and spatial decrements in the right eye.

3.2. Results

The dichoptic experiment measures when the motion signal in one eye is nulled by a motion signal in the other eye. The expected results differ according to whether the equal-motion signals occur because (a) each eye's bar has the same absolute luminance difference from their respective surround (the linear explanation) or (b) each eye's bar has the same Weber contrast (the non-linear explanation).

We shall first describe the characteristic pattern of *hypothetical* results with respect to our graphs if either a linear or Weber contrast story holds. First, a note explaining how to interpret our graphs (Figs. 3 and 4). Results are shown as a series of curves. The parameter for each curve is a particular stimulus seen by the left eye (defined by the left eye bar luminance and surround). Any datum point on that curve shows an 'equal-motion' right eye stimulus, namely a combination of surround luminance (x-axis) and bar luminance (y-axis) which when seen by the right eye just cancelled out the motion signal seen by the left eye. Each line on the plot connects the datum points which had equal-motion strength to a particular left eye bar and surround luminance combination. Such a curve is an isomotion contour or curve. The positive diagonal (dashed) shows stimuli of zero contrast for which the bar and surround have equal luminances. Curves above the positive diagonal represent right eye equal-motion spatial increments, and curves below the positive diagonal represent right eye equal-motion spatial decrements.

A *linear* scaling of bar and surround luminance on double-linear co-ordinates would mean that a motion signal in one eye could be balanced by the other eye's motion signal as long as that signal's bar luminance excursion from the surround was the same (equal absolute luminance difference). A line passing through all the different bar and surround luminance combinations in one eye that were equal in motion strength to a given combination of bar and surround luminance in the other eye should run parallel to the positive (zero contrast) diagonal. The intercept on either the x- or y-axis of this parallel line would be the difference in luminance between bar and surround (Fig. 3b). On double-log co-ordinates, these parallel lines become bowed curves stretching from the intercept on the x- or y-axis (equal to the luminance difference between bar and surround) to the top-right corner of the positive diagonal (Fig. 3c). *Hypothetical* combinations of right eye bar and surround luminances (cd/m^2) that would satisfy a linear relationship are (a) 45:30; (b) 25:10; (c) 25:40 and (d) 5:20 (cf. Fig. 3b, c).

For a *Weber contrast* scaling of bar and surround luminance, on double-linear co-ordinates, a line passing through all the different combinations of bar and surround luminance that balance another eye's motion signal would lie along a straight line anchored at the origin. The line represents motion signals of constant Weber contrast (equal-ratios). The slope of the line indicates the amount of contrast, with lines deviating further from the positive diagonal having higher contrasts (Fig. 3d). If these lines are replotted on double-log co-ordinates they become parallel lines (Fig. 3e), with increasing distance from the positive diagonal (instead of increasing angle) corresponding to increasing Weber contrast. *Hypothetical* combinations of right eye bar and surround luminances (cd/m^2) that would satisfy a Weber contrast relationship are (a) 45:30; (b) 15:10; (c) 20:40 and (d) 10:20 (cf. Fig. 3d, e).

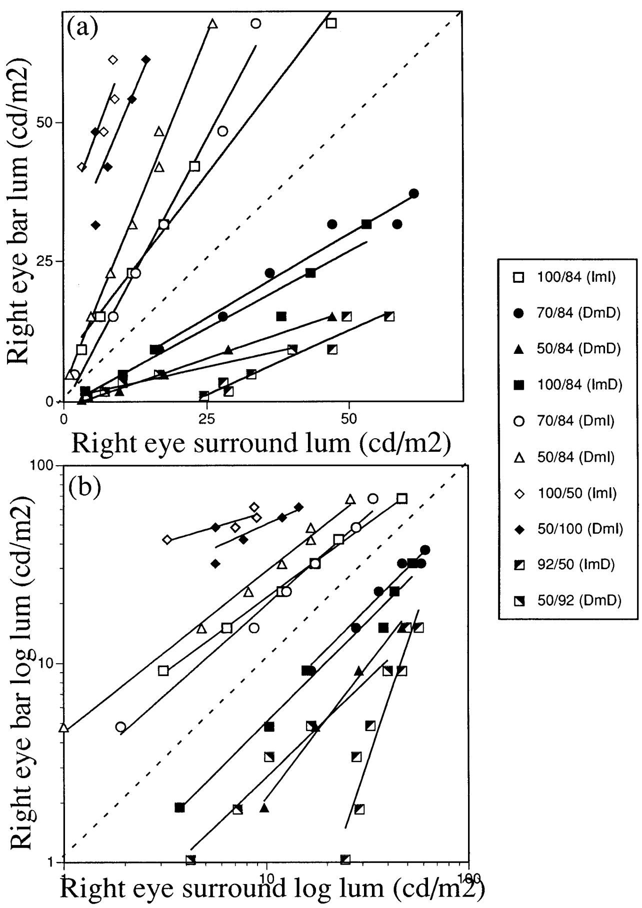

Fig. 4. Results for experiment 2. Lines connect data points which had the same motion strength. Data are plotted on double-linear co-ordinates (a) and again on double-logarithmic co-ordinates (b). If equal Weber contrast gave equal-motion strength, all the curves on the double-log plot would be straight parallel lines with a slope of + 1. This is largely true, except for extreme values where they taper inwards and upwards, showing that less contrast is needed at higher mean luminances in order to conserve motion strength.

Our actual results are plotted in Fig. 4 twice, on double-linear (Fig. 4a) and on double-log (Fig. 4b) co-ordinates. The linear co-ordinates plot shows the isomotion contours as fanning out from the origin. The logarithmic co-ordinates plot confirms this with the isomotion contours running approximately parallel with the zero contrast line (the dotted positive diagonal). Clearly our data are consistent with the luminance differences between the bar and surround being normalised by the surround. *Equal Weber fractions give equal-motion strengths* (cf. Eq. (4)). Our data show that luminance processing for apparent motion signals in our second experiment is highly non-linear. The linear behaviour in our first experiment presumably arose because of the visual parsing of the display into separate ON- and OFF-signals which were subsequently equated.

Examination of the double-log plot shows that not all the isomotion contours are parallel to the zero contrast positive diagonal (Fig. 4b). This fall-off from Weber-like behaviour is marked for the high contrast targets where there is a convergence inwards towards the positive diagonal as one goes up and to the right. As the overall luminance level increases, less Weber contrast is necessary to conserve equal-motion strength. Look at the extreme right-hand bottom curve in Fig. 4(b) which represents dark bars on very light surrounds. The curve has a slope of 3, meaning that a unit (log) change in the bright surround needed a (log) change of 3 in the dark bar to compensate. Now look at the left-hand uppermost curve in Fig. 4(b) which represents very light bars on dark surrounds. The curve has a slope of 0.3 meaning that a unit (log) change in the bright bar needed a (log) change of 3.3 (= 1/0.3) in the dark surround to compensate. In other words, the lighter region within each stimulus was almost three times as important as the darker region in setting the motion strength, and it made little difference whether it was the bar or the surround that was lighter. This preponderance of the lighter region was true to a lesser extent for every stimulus in the experiment, insofar as the slopes of the spatial increment curves were less than one, and the slopes of the spatial decrement curves were greater than one. This disproportionate favouring of the lighter region over the darker region might arise whenever the visual system is presented with a visual scene containing a mixture of light and dark patches. We conjecture that the luminance level of the lighter region sets the adaptation level — the visual system becomes light-adapted, not dark-adapted. This is an important question which deserves further investigation.

As a quick demonstration of the rôle of adaptation state upon motion strength, we re-examined the indifference situation in which the bar luminances were 1 and 100% (where 100% equals 67.8 cd/m^2) and the surround was 50%. We put one bar into each eye, such that the left eye saw a white bar (100%) on a grey surround (50%), while the right eye saw a black bar (1%) on a similar grey surround (50%). Not surprisingly, indifference was conserved and no net motion was seen. We now put a one log unit neutral density filter over the left eye, which moved the operating point of that eye down and to the left. The right eye now dominated and the black bar was seen as jumping. We now transferred the filter from the left to the right eye. The left eye now dominated and the white bar was seen as jumping. Of course the filter reduces the mean luminance level but does not alter the Weber contrast ($\Delta I/I$), so this observation confirms the finding shown in Fig. 4 that a slightly dark-adapted eye needs more contrast to maintain a given motion strength.

The slopes of the high contrast data (both increments and decrements), as a group, seem to be substantially steeper than the low contrast data. We quantfied this difference statistically. We divided the data into two sets — low contrast data (Weber contrast ± 16, ± 20 and ± 40%) and high contrast data (± 84 and $\pm$ 100%). We fitted best fitting lines to each condition. The slopes of the lines were used in an analysis of variance (one-way classification). The F-ratio (0.1753) with numerator $df = 1$ and denominator $df = 9$, did not reach significance level. Therefore the slopes fitted to the high contrast and low contrast data, as a group, do not appear to differ significantly from each other. A further sub-analysis compared the slopes of just high contrast right eye equal-motion spatial *increments* (curves above the positive diagonal cf. Fig. 4), against the low contrast data slopes. The F-ratio (14.5264) with $df = 1$ (numerator) and $df = 7$ (denominator) was statistically significant ($P < 0.01$). The slopes for high contrast right eye equal-motion spatial *decrements* (curves below the positive diagonal) were not significantly different from the low contrast slopes (F-ratio (4.5809), numerator $df = 1$ and denominator $df = 7$). At the moment we are unclear as to why high contrast spatial increments should differ from the rest of our data in this experiment. Possibly the effect of higher luminance levels, where the lighter region is weighted more than the darker region, might complicate our interpretation of this particular result.

Whereas experiment 1 measured the indifference point only for the special case of equal-motion signals from the light and dark bar against the same surround luminance, we have now generalised it so that a light or dark bar motion signal in one eye can be nulled by a number of different light or dark bars of different luminances and surrounds. We have shown that bars of equal Weber contrast had equal-motion strengths whatever the absolute values of their surrounds (though this is modified for higher luminance levels where the lighter region, whether bar or surround, is weighted more than the darker region).

3.2.1. Control against fusion-before-motion

There are two possible objections to our dichoptic motion experiment. First, it might perhaps be that the grey surrounds seen by each eye were averaged binocularly *before* motion was processed (fusion-before-motion). Thus, a light grey surround seen by one eye might be binocularly combined with a dark grey surround seen by the other eye, to produce a binocular mid-grey which was a weighted average of the two monocular grey surrounds (Anstis & Ho, 1998). In this case there might be only one effective surround instead of two. Second, interpretation of the experiment is complicated for the opposite reason, i.e. instead of fusion occuring before we wanted it, perhaps it never occurred when the left- and right eye's monocular percepts were too different (binocular rivalry). This could have occured when either the surround luminances in the two eyes were very dissimilar and/or when there were different interocular contrast polarities. We address the problem of binocular rivalry in the next section (cf. experiment 2a).

We performed a control experiment designed to prevent fusion-before-motion by promoting binocular rivalry. Three conditions were used (Fig. 5): (a) each eye simply saw a separate bar on its own surround (a repetition of experiment 2); (b) the field seen by each eye was overlaid with a set of identical oblique black and white pinstripes; and (c) the pinstripes were made orthogonal in the two eyes, being left-oblique in one eye and right-oblique in the other eye, so that they could not be fused binocularly but instead tended to promote binocular rivalry. The control condition (b) merely checks that adding pinstripes has no unwarranted side-effects upon our results.

The left eye always saw a bar of luminance 28 cd/m^2 superimposed on a surround of 54 cd/m^2 (Weber contrast $(\Delta I/I) = (54 - 28)/54 = 0.48$). This decremental bar jumped back and forth in apparent motion. The right eye saw a bar that jumped back and forth in counterphase to the left eye bar , as in our dichoptic motion experiment. The experimenter set the luminance of the right eye's bar on different trials to one of nine luminance values ranging from 20 to 100 cd/m^2, and the observer selected a surround luminance for the right

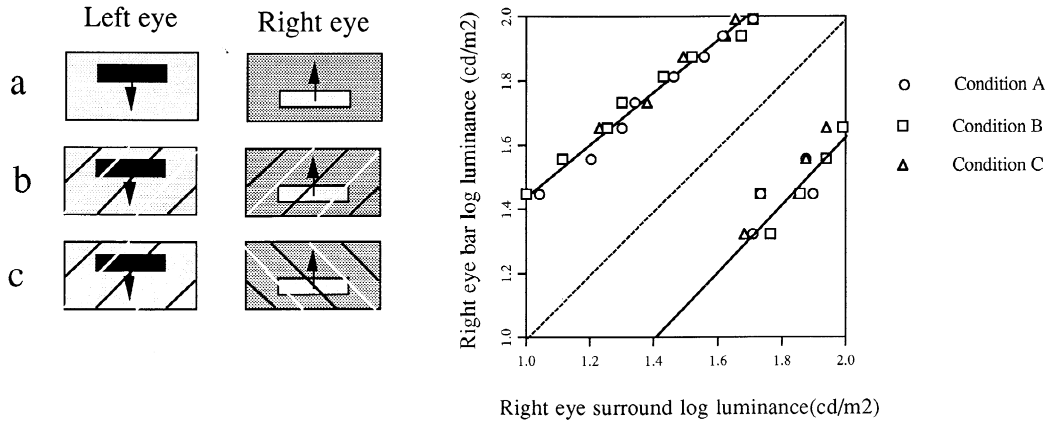

Fig. 5. Diagram of stimuli and results for control experiment examining fusion-before-motion. The left eye saw one bar jumping repetitively back and forth. The right eye saw a bar that jumped back and forth in counterphase to the left eye bar . The views of the two eyes were fused binocularly (if possible). The experiment consisted of finding a set of right eye bars, both increments and decrements whose upward motion just cancelled out the left eye's downward motion. (a) Each eye saw a separate bar on its own surround (this is a replication of experiment 2). (b) The field seen by each eye was overlaid with a set of identical oblique pinstripes (control to ensure that adding pinstripes has no unwarranted side-effects). (c) The pinstripes were orthogonal in the two eyes thus promoting binocular rivalry. (d) The graph shows the results for one observer (SA). Lines connect data points which had the same motion strength. Data are plotted on double-logarithmic co-ordinates (for interpretation of graph cf. Figs. 3 and 4).

eye that just caused the fused motion to cancel. Settings were made in all three conditions for both incremental and decremental bars presented to the right eye. All of the details were the same as in our previous dichoptic motion experiment.

Results are shown for one observer SA (mean of three readings per datum point) on double-log co-ordinates (Fig. 5). It will be seen that all the results obeyed the same rules as in our dichoptic motion experiment, such that the datum points for all incremental and decremental stimuli of the same motion strength fell along two parallel lines in the log–log plot, indicating as before that equal Weber fractions give equal-motion strengths. Furthermore, the result from all three conditions lay along the same curves, showing that the prevention of binocular fusion of the luminance did not alter the results. We conclude that binocular fusion of the two eyes' surrounds did not occur before motion was computed in each eye.

Though none of our observers reported binocular rivalry we can not be sure that binocular rivalry might not have occurred (the use of opposite motions in the two eyes is known to promote binocular rivalry, e.g. Fox & Check, 1968). The possible presence of such interocular phenomena would cloud the interpretation of our dichoptic motion experiment, and would consequently weaken the confidence with which we could extrapolate from experiments involving dichoptic presentation to experiments involving binocular presentation.

We could think of no change in experimental design that would enable us to rule out binocular rivalry effects in our dichoptic motion experiment. We therefore decided to explore another spatial task (Vernier offset) where each stimulus was associated with different surrounds but where the presentation was binocular. *If* we get results in accordance with Weber contrast scaling of luminance (straight lines fanning out from the origin in double-linear co-ordinates), then we have direct evidence for non-linear compression of luminance in a Vernier task. As both experiment 1 and 2a used binocular presentation, this would allow us to argue that linear processing of luminance in experiment 1 was only apparent (arising from equal and opposite non-linearities cancelling out in the ON- and OFF-spatial pathways). The similar results between experiment 2 and 2a would also enable us to have reasonable confidence in arguing for the relevance of our dichoptic motion experiment in explaining effects (i.e. apparent linearity) observed in our binocular motion experiment.

4. Experiment 2a

The Vernier offset discrimination task was modified to allow different surrounds to be associated with different Vernier lines. Examples of the Vernier stimuli used in experiment 1 (cf. Fig. 1b) should be compared with our new Vernier stimuli (cf. Fig. 6a). The difference is that the new Vernier stimulus allows one bar to be placed next to one surround while simultaneously the other bar is placed next to another different surround. This was not possible in experiment 1.

4.1. Methods

The stimuli were generated on a Silicon Graphics O2™ workstation and displayed on a colour graphics

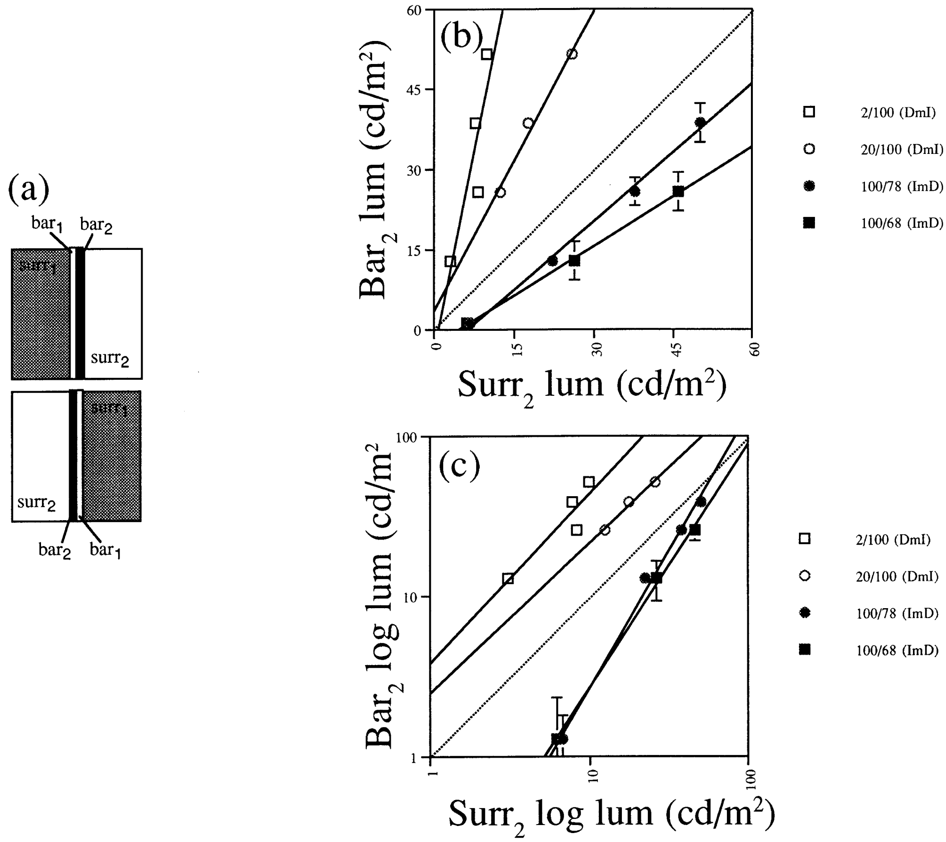

Fig. 6. Diagram of stimuli and results for experiment 2a. (a) One panel (of 30 arranged in a 3 × 10 matrix) is shown. The Vernier offset display possesses two different surrounds (surr1 and surr2) which should be compared with the previous Vernier display which only had one surround (cf. Fig. 1b). (b, c) The graphs show the averaged data from two observers (two readings per observer). Error bars represent ± 1 S.E. of the mean. The same data is replotted on double-linear and double-logarithmic co-ordinates (b and c, respectively) (for interpretation of graphs cf. Figs. 3 and 4).

display. All observations took place in a darkened room using a viewing distance of 57 cm. Two subjects (the second author and an observer näive to the purpose of the experiment) took part in this experiment. The display consisted of a 3 × 10 matrix of 30 panels which were presented upon a uniform grey background subtending an area 29.3° wide by 22.7° high, and having a luminance of 33 cd/m^2. Each panel consisted of an upper and lower pair of lines (cf. Fig. 6a). The stimulus can be thought of as a light Vernier target with the upper line displaced to the left, superimposed on a dark Vernier target displaced to the right. Which of these two opposed percepts dominates depends on the luminance of the surround (cf. results from experiment 1).

The vertical line stimuli (bar 1 and bar 2, cf. Fig. 6a) were 4.1 min arc wide by 2.28° high. Each surround (surr1 and surr2) measured 1.14° wide by 2.28° high. The upper and lower line pairs were separated by a 13.67 min arc vertical gap. Each upper and lower line pair consisted of two contiguous vertical lines. The luminance values of the surr2 areas of the panels varied from 0.0 cd/m^2 (black) at the top-left to 59.8 cd/m^2 at the bottom-right, in steps of 2 cd/m^2. Luminances were measured using a Macam L103 photometer.

For each trial, bar 1 and surr1 were pseudo-randomly chosen by computer from one of four combinations of bar and surround luminance thus creating decremental and incremental Vernier stimuli of Weber contrast − 98, − 80, + 28 and + 47% (bar to surround luminance (bar:surround) of 2:100, 20:100, 100:78 and 100:68, respectively, in percentages where 100% (white) was equal to 66 cd/m^2). On each trial, the value of bar 2 was pseudo-randomly chosen by computer from one of five values (2, 20, 39, 59 and 78% where 100% = 66 cd/m^2). The task of the observer was to select the panel where there was no percept of Vernier offset. This marked the indifference luminance point for this task. The average of two readings for each condition were used.

4.2. Results

Results are plotted in Fig. 6 twice, on double-linear (Fig. 6b) and on double-log (Fig. 6c) co-ordinates. The linear co-ordinate plot shows the isovernier contours as fanning out approximately from the origin. This is behaviour consistent with luminance differences between bar and surround being normalised by the surround, i.e. Weber contrast scaling of luminance. If luminance was processed linearly in this task then the curves would have been parallel to the positive diagonal when plotted on double-linear co-ordinates. This is clearly not the case. The double-log co-ordinate plot (Fig. 6c) confirms the Weber scaling interpretation of luminance for points above the dotted diagonal line (decrements matched to increments), as Weber contrast scaling predicts data should fall along straight lines parallel to the positive diagonal when plotted on double-log axes. The intrepretation of points below the line (increments matched to decrements) is less clear. There is a fall-off from Weber-like behaviour (though note the behaviour is certainly not consistent with linear luminance processing which predicts bowed curves in double-log co-ordinate plots, cf. Fig. 3c). We found similar behaviour in our dichoptic motion experiment (cf. Fig. 4). We attributed the departure from expected behaviour in the dichoptic motion experiment as being due to the disproportionate favouring of lighter regions over darker regions when the visual system is presented with a visual scene containing a mixture of light and dark patches. We suggested that this arose because the visual system becomes light adpated not dark-adapted. We apply the same reasoning to our Vernier offset discrimination task.

The results from experiment 1 suggested that luminance processing was linear in a Vernier offset task. We have now shown that the processing of luminance in a Vernier offset task follows a Weber contrast rule. This is a hallmark of non-linear compression and we suggest that the linearity in experiment 1 was only apparent. We consider the close agreement between data from our complex Vernier task (experiment 2a) and our dichoptic motion task (experiment 2), as evidence that the dichoptic motion task can also be used to support our reasoning that luminance is processed non-linearly in separate ON- and OFF-spatial pathways.

5. Experiment 3

Our binocular and dichoptic presentation of various stimuli has taught us some important lessons. We know that motion and Vernier signals with equal Weber fractions (contrast) generate equal-motion and Vernier strengths. This is to say, that luminance differences (ΔI) between stimuli and surround are normalised to the context (I) within which the signals are seen. Second, if presented with separate ON- and OFF-signals, the visual system seems to parse the display into signed luminance signals and balance out (cancel) the signal strengths within each signed luminance pathway. Can we use this knowledge to explain an intriguing finding of Whittle's (1992), that equal steps in brightness follow Weber's Law ($\Delta I/I$) with respect to luminance at high contrasts (consistent with brightness being proportional to the log of stimulus luminance), but with respect to the difference in luminance between the stimulus and the surround ($I-\Delta I$) at low contrasts?

Consider when observers are shown a series of simultaneously present panels and are invited to adjust the luminances of the n panels so as to form a series of equal step differences in brightness ranging between the two extreme luminance values of the series L_1 and L_n. The series of panels are superimposed upon some constant surround luminance L_{Surr} (where $L_1 > L_{\mathrm{Surr}} < L_n$). Though the observer is performing a 'global' task (the goal is for the whole series to shade smoothly from one given luminance to another, say black to white with all the intervening greys), the task is performed at the 'local' level (the change in brightness between any two panel pairs should be subjectively the same anywhere along the series). For most local decisions the observer operates within the same ON- or OFF-pathway for the two paired panel luminances. This is certainly the case for high contrast signals which represent ON- and OFF-signals by definition far-removed from the surround luminance. When two panel luminances are processed in the same ON- or OFF-pathway then both luminances pass through the same non-linearity (cf. experiments 2 and 2a). Therefore at high contrasts we would expect brightness perception to follow Weber contrast with respect to panel luminance. However, there must exist one step of brightness that straddles the surround luminance (if $L_1 > L_{\mathrm{Surr}} < L_n$). If equal and opposite non-linearities cancel out when the visual system is able to parse the display into ON- and OFF-signals (cf. experiment 1) then this particular brightness step might well require a smaller luminance difference compared with the steps in luminance required for neighbouring panels in the series. The step will be smaller because the balance of signals occurs around a common normalisation level (the surround luminance), and observers would be measuring off subjective magnitudes at the lower end of the logarithmic compression scale thus requiring less physical luminance differences to get a criterion response. This explanation would predict a sharp minimum in the luminance step between the panels *only* for the luminance panel pair straddling the surround luminance. However, Whittle (1986, 1992) reports that heightened discrimination or reduced luminance magnitude for brightness steps, reach a maximum around the surround luminance but are present though diminishing in size of effect up to approximately $\pm L_{\mathrm{Surr}}/2$ cd/m^2 of the surround luminance. How can we subsume this wide range over which the effect occurs within our explanation, given that the effect is present for panel luminance pairs which are exclusively increments or decrements?

The relatively wide range over which brightness is proportional to luminance difference could be explained within our scheme of equal and opposite non-linearities cancelling out, if we consider that the observer, in order to set a grey-series of equal brightnesses, might partition the grey-series at more than one spatial scale. The local luminance panel pair might represent the finest or highest spatial scale within the context of the task. The coarsest scale might simply partition half the grey-series into ONs and OFFs relative to the surround luminance. In between these two spatial scales (fine spatial panel luminance pairs and coarse spatial whole series), the observer might have access to a number of bisections of the task at different spatial scales. The neural machinery subserving these representations could be carried by ON- and OFF-spatial luminance pathways tuned to a number of different centre spatial frequencies. Physiological (e.g. De Valois, Albrecht & Thorell, 1982) and psychophysical (e.g. Campbell & Robson, 1968) evidence for such channels is strong. If weighting was inversely proportional to increasing size of spatial scale, we might expect parsing of ON- and OFF-signals to occur maximally at the finest scale (the luminance step straddling the surround luminance) but to fade off in strength as a function of step distance from the straddled luminance pair. At a certain retinal distance it would be natural for the parsing of the series into ON- and OFF-signals to be unwarranted (the series within the foveal visual field will all be clearly ON- or OFF-signals), at which point the series luminances will be processed non-linearly. We appreciate that this implies that the change over from linear to non-linear luminance processing might depend upon the scale of the display. We however do not pursue this particular aspect in this paper. Whittle suggested that his results 'represented a change over from luminance to contrast coding in the retina' (Whittle, 1992), and we think we see the mechanism by which it occurs.

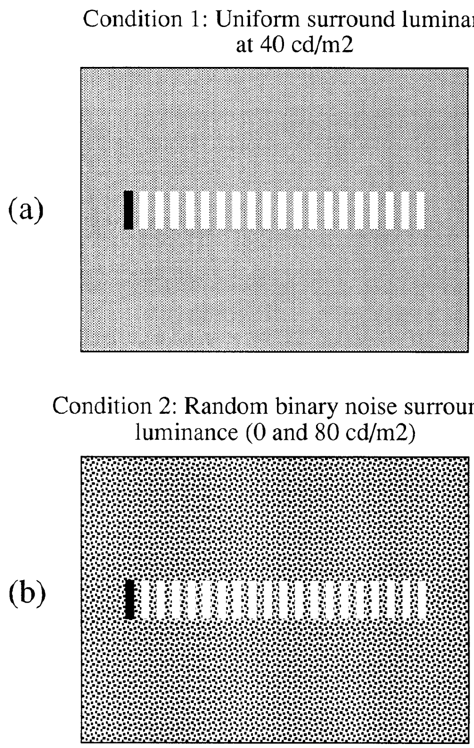

Fig. 7. Diagram of the stimuli in experiment 3. (a) Condition 1. Twenty panels were presented arranged in one horizontal row. The panels were centred against a uniform grey surround (40 cd/m^2). The leftmost panel and rightmost panels had a fixed luminance (0 and 80 cd/m^2, respectively). The observer's task was to adjust the luminances of the in-between panels so that the series shaded smoothly from black to white, with equal differences of brightness between each panel. (b) Condition 2. The panel luminances and task were the same as for Condition 1. The difference between the conditions was that the surround was random binary noise (50% chance that the dots were 0 or 80 cd/m^2).

We wanted to see if we could force observers to partition a series of panels, in a task of judging differences in brightness, in an (apparently) linear fashion. This could be seen as an 'ironing-out' of the pronounced 'dipper' function (less luminance needed to achieve a just noticeable difference between two luminances when those luminances are near to the surround luminance) seen in Whittle (1992). To achieve this we reasoned that we needed to make each panel, simultaneously with all the other panels, both an ON- and OFF-signal.

There were two conditions. The first condition required observers to set a series of panel luminances so that the series, as a whole, appeared to shade smoothly from black to white. The step difference in brightness between each panel was meant to be the same across the whole series. The (uniform) surround luminance was set at the arithmetic mean of the leftmost (black) and rightmost (white) panel luminances. This condition was essentially a repeat of Whittle's (1992) main experiment (though the particular stimuli and details were different), and was undertaken to check that our observers showed the same switch in brightness perception at luminances near to the surround luminance (perception proportional to luminance difference, rather than following Weber contrast). The second condition required observers to perform the same task of setting a grey-series of equal brightness steps, with the difference that the surround now consisted of a dense pattern of random stationary dots (half white and half black). This made each panel an ON- and an OFF-signal, relative to the sets of different luminance dots.

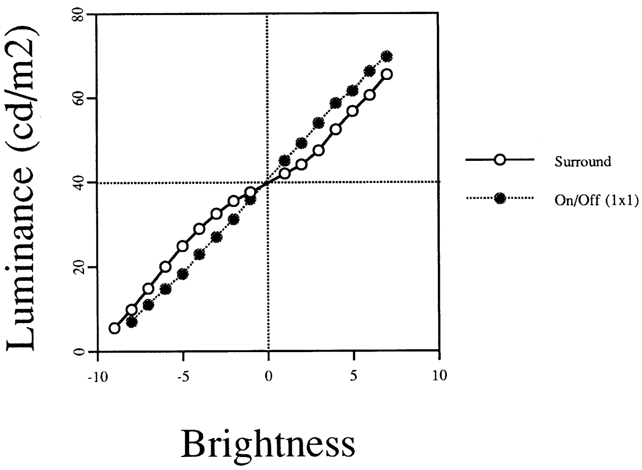

Fig. 8. Results for experiment 3. An equal interval brightness scale for 20 grey panels on either a uniform grey surround of 40 cd/m^2 (open circles) or a dense binary-noise (black = 0 cd/m^2 and white = 80 cd/m^2) surround, plotted against luminance. The ordinate unit is in terms of ordinal numbering of the panels with the zero shifted, i.e. the leftmost panel (cf. Fig. 7) is −10 and the rightmost panel is +10. The results are the average of four observers.

5.1. Methods

The stimuli, which are shown in Fig. 7, were generated on a Silicon Graphics O2™ workstation and displayed on a GDM-17E21 colour graphic display. The frame rate was 75 Hz, with a horizontal line frequency of 79.5kHz. Each panel subtended an angle of 0.5° wide by 1.5° long at the viewing distance of 57 cm. The gap between the outer and inner edges of each neighbouring panel was 0.65°. There were 20 panels aligned in a single horizontal row, centred in the middle of the screen, subtending an angle of 22.4° (from the outer edges of the leftmost and rightmost panels). The leftmost panel luminance was fixed at black (0.35 cd/m^2) and the rightmost panel luminance was fixed at white (79.5 cd/m^2). These luminances were the lowest and highest luminances obtainable on the monitor. Each panel was distinguished from the surround solely in terms of its luminance difference from the surround (there was no outline border around the panel cf. Whittle, 1992). The stimuli were presented against a surround field which occupied the whole of the monitor display area and measured 29.3° wide by 22.7° high. The luminance of the surround was either set to a uniform 40 cd/m^2 (Condition 1, see Fig. 7a), or consisted of a dense pattern of stationary randomly-positioned dots (Condition 2, see Fig. 7b). Each dot was a pixel in size (subtending an angle of 0.025° or 1.5 min arc), and had a 50% chance of being either black (0.35 cd/m^2) or white (79.5 cd/m^2). Luminances were measured using a Macam L103 photometer.

Initially all the panel luminances (except the first and last panel which were fixed throughout the experiment), were randomly set by the computer program. The task was to adjust the luminances of all the in-between panels to make an equal interval brightness scale. How this was done was left to each observer though observers were told to try and generate a smooth change in brightness between the black and white panels. The left and right arrow-keys on a keyboard were used to move freely between the panels. The up and down arrow-keys were used to raise or lower the luminance of each panel (in 1/255 resolution steps). Observers took as long as they liked to set a series (DRRS took about 15 min). When the observers were happy with the series they pressed a mouse-button to record the luminances. The panel luminances were then randomly set again. The average of three runs for each observer were used. The four subjects were the second author (DRRS) and three observers näive to the purpose of the experiment.

5.2. Results

Our results are shown in Fig. 8, with the brightness scale (abscissa) plotted against linear luminance (ordinate)[1]. The abscissa represents the numbering of the panels with the zero shifted so that brightness is zero when luminance matches the surround luminance. As half the panels were set to be decrements and half were set to be increments, then panel number 1 (or −10 ordinate) would be the strongest decrement and panel number 10 (or −1 ordinate) would be the weakest decrement. For increments, panel number 11 (or 1 ordinate) would be the weakest increment and panel number 20 (or 10 ordinate) would be the strongest increment. The ordinate shows the panel luminances set by the observers to form an equal interval-scale of brightness. Data are averaged across the four observers for each condition.

Consider the data for the first condition (open circles) where observers set the grey-series against a uniform surround luminance of 40 cd/m^2 (halfway between the anchor points $L_1 = 0.35$ cd/m^2 and $L_{20} = 79.5$ cd/m^2 for the series). The reduction in slope of the curves where they pass through the surround luminance shows the basic effect. Starting from the left and proceeding to the right along the series, we see at first that a greater luminance difference between each panel is required to produce the same unit change in brightness (brightness is proportional to the logarithm of luminance). Equal Weber contrast steps generate unit steps in brightness. This shows as a positively accelerating curve. However, as the panel luminances approach that of the surround luminance, i.e. the panel luminances become weaker

[1] Comparison between our results and Whittle's (1992) results is somewhat complicated because Whittle plots the dependent variable along the abscissa in common with the scaling literature convention. We have not decided to adopt this particular convention.

and weaker decrements, then the slope of the curve reduces. This means that less and less difference is needed to have the same change in brightness as panel luminance nears surround luminance (brightness is proportional to luminance difference). After the panel luminance passes through the surround luminance (momentarily vanishing) then we see a symmetrical effect for increments. The stronger the panel increment (further from the surround luminance) then the greater the difference needed to have a unit step change in brightness. This represents a switch from brightness perception depending on luminance difference to being a function of the log of luminance, that is to say following Weber contrast (reading from left to right). This effect is characterised by a reduction in slope of the curve as panel luminance passes through surround luminance, or equivalently the clustering of the data points around surround luminance. The results from this experiment repeat Whittle's (1992) main effect.

More interesting is the second condition (solid circles). Observers again set a grey-series constrained to run in brightness between black and white. However, this time the task was performed against a surround consisting of a dense pattern of black and white dots. Note that the reduction in slope (and subsequent kink around surround luminance) of the curve seen in the first condition (uniform surround luminance), is abolished. The data points are strung along the curve at approximately equal intervals thus confirming that now observers set the *whole* series in a way consistent with brightness perception being a function of luminance difference.

We interpret the linear behaviour in the black and white dot condition, as being a consequence of the dots making each panel simultaneously an ON- and OFF-signal. The observer must partition the panels with effectively two surround luminances (the two sets of different luminance dots) where each surround lies at the end-point of the series. When an observer sets the luminance of a panel s/he might have access to the relative ON- and OFF-pathway activation generated by the panel luminance vis-á-vis the two sets of dots. This extra information might help to 'linearise' the grey-series because the visual system will always be balancing the two different pathway activity levels at a lower end of the logarithmic compression scale than if it were measuring the activity in only one luminance pathway (as in the uniform surround luminance condition).

6. General discussion

Let us review our main experimental findings. Our experiments pitted spatial signals of opposite luminance polarities against each other, in the domains of apparent motion, Vernier discrimination, and stereoscopic depth discrimination. The subject's task was essentially to bisect the luminance of the light and dark bars to find an indifference luminance for the surround at which the phenomena of motion, Vernier offset or stereoscopic depth reached a minimum.

6.1. Experiment 1

We found that in motion, Vernier and stereoscopic depth bisections, our subjects selected a null surround which lay at the arithmetic mean of the bar luminances. Thus if the bar luminances were 1 and 100, subjects set the null surround to 50.5 (the arithmetic mean), not to 10 (the geometric mean). This suggests that the visual system operated linearly upon the raw luminances.

However, the linearity of the system might only be apparent. The results from our first binocular experiment certainly preclude a non-linear compression if all the signals are processed in the same pathway. Yet the results could be explained using a non-linear compression if the two signals (bisected by the common surround) are processed within separate luminance polarity (ON or OFF) specific pathways, and are subsequently subtracted from each other.

6.2. Experiment 2

This set of experiments explored the issue of non-linear compression by isolating each bar against a different surround. This was achieved by dichoptically presenting different surrounds to different eyes (for the apparent motion task), or by spatial manipulations of the binocularly viewed display (for the Vernier offset discrimination task). We showed that two bars have the same percept strength if they have the same Weber contrast ($\Delta I/I$). Thus for the motion task, a left eye bar of 10 cd/m^2 presented on a left eye surround of 20 cd/m^2, could be balanced by a right eye bar of 5 cd/m^2 presented on a right eye surround of 10 cd/m^2 (or indeed by any right eye bar and surround combination with a positive or negative Weber contrast of 0.5).

6.3. Experiment 3

This experiment addressed why brightness perception should be linear at low contrasts but logarithmic at high contrasts (Whittle, 1992). We showed that observers set the series in a fashion consistent with brightness perception being a function of linear luminance for all contrast levels when the surround was a dense pattern of black and white dots. The random binary-noise surround made each panel simultaneously an ON- and OFF-signal. Making each panel both an ON- and OFF-signal potentially allowed observers access to the ON- and OFF-pathways' relative activation level. This would have enabled the visual system to compare activity levels at the lower end of the logarithmic compression scale than would have been the case for signals analysed solely within one luminance pathway.

Whittle (1992) also reported that the Crispening Effect was greatly reduced by either of two stimulus changes: by enclosing each stimulus patch (disks instead of vertical bars) with a thin (2 min arc) black pixel outline; or by creating a hue difference between circles and surround. Whittle suggested that the outline reduced the effect because outlines are known to impair both luminance discrimination (Walsh, 1958) and the perception of suprathreshold luminance differences (Tolhurst, 1972). Whittle also suggests that hue differences reduce the Crispening Effect because chromatic contrast masks achromatic luminance differences (Switkes, Bradley & De Valois, 1988). If the discrimination performance of ON- and OFF-spatial pathways is impaired by the presence of an outline or hue difference then this might cause a mismatch in the cancellation of the opposite non-linearities carried in the ON- and OFF-spatial pathways, leading to an obscuration of the effect at near-threshold luminances. Further work is needed to address this particular point.

6.4. A common underlying pathway for spatial vision?

The results in our first experiment explored luminance processing in three quite different spatial vision tasks: motion discrimination, Vernier acuity and stereoscopic depth discrimination. Across the three tasks the results were the same (Fig. 2), namely apparent linearity of response to stimulus luminance. We attribute this close agreement across tasks to equal and opposite non-linearities cancelling out (experiment 2) perhaps based upon a common and early neural substrate of ON- and OFF-spatial luminance cells.

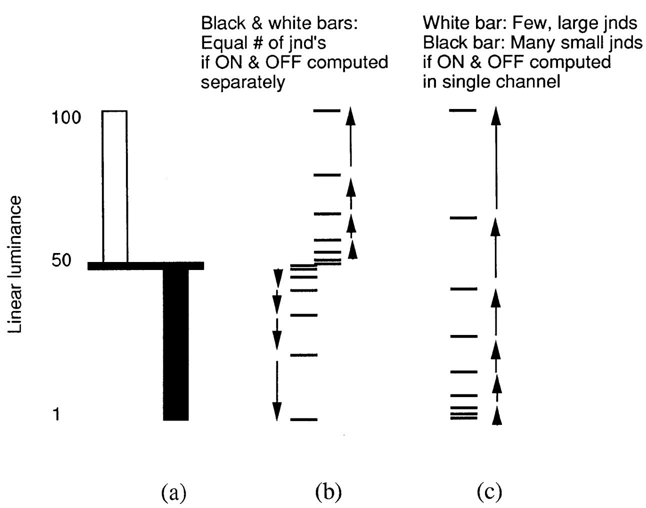

Fig. 9. (a) Dark and light bars of equal-motion strength presented upon an intermediate grey surround (1, 100 and 50 arbitrary luminance units, respectively). Just noticeable differences are (b) equal if the motion signals are computed in separate luminance ON- and OFF-pathways, but (c) unequal if the motion signals are computed in a single unsigned luminance pathway. Each jnd is shown schematically as a horizontal line, with the arrows showing the signed dimension along which the jnds sum.

6.5. Implications for Weber and Fecher Laws

In our first set of experiments subjects set the surround luminance at the arithmetic mean of the luminances of the two competing stimulus' luminances to achieve equal strength percepts. If all luminances (both stimuli and the surround) were processed within the same pathway this would contradict Fecher's claim that internal response strength was proportional to the logarithm of stimulus luminance. Furthermore, Fechner proposed that differences in internal response strength could be summed as just noticeable differences (jnds). But a linear relationship between stimulus luminance and surround means that the lower luminance stimuli has more jnds to the surround luminance value than the higher luminance possesses. The classic explanation for this effect would be that jnds are *not* perceptually equivalent regardless of their place on the sensory scale (for a full discussion cf. Laming, 1986). We suggest a simpler explanation, that light and dark bars of equal-motion strength do have an equal number of jnds if the display is parsed into separate ON- and OFF-signals (Fig. 8). The surround luminance provides the gain control mechanism within each signed luminance pathway with the same fixed operating point, and the signed dimensions increase away antagonistically from this fixed point. This equalising of the number of jnds provides strong, if indirect, evidence that ON- and OFF-pathways are computationally separate, which in turn suggests that they may be physiologically separate.

The link between perceptual strength and jnds can be generalized to different luminance surrounds. Whittle (1992) tested conditions where the surround was either uniform black or uniform white. This necessitated observers to set a series that was either all increments or all decrements, respectively. Observers showed a similar switch (as seen when the surround luminance was intermediate to the two end-point panel luminances) from following Weber's Law with respect to luminance at high contrast, to following a scheme where brightness appears to be a function of luminance difference at low contrast. This could be attributable to the physical luminance difference necessary to generate a jnd increasing as observers set a grey-series, i.e. jnds closer to the fixed operating point set by the surround luminance would be smaller in luminance steps (Fig. 9).

6.6. Implications for the gain symmetry of the ON- and OFF-pathways

The fact that our first set of experiments so closely mimic linear behaviour implies that the luminance transforms within the ON- and OFF-pathways are similar. If the systems were anything other than nearly symmetrical we would have expected our results to deviate from linearity.

6.7. Why have two luminance specific pathways?

Given that the visual system could theoretically signal luminance increments and decrements by excitatory and inhibitory changes in neuronal firing rate within a single unsigned luminance pathway, we might ask why there are two anatomically distinct subsystems (Kuffler, 1953) co-existing in the visual system. What benefits could such a parallel organization of the system provide? We follow the reasoning of Fiorentini, Baumgartner, Magnussen, Schiller and Thomas (1990).

The advantages are likely to lie in the opportunities for optimizing transmission of information about the time-varying spatial patterns that are the input of the visual system. This can be quantified as improvements in the signal to noise ratio across a wider dynamic linear range at lower metabolic cost than would be possible for a system using only a single unsigned luminance pathway (Bayly, Cervetto, Fiorentini & Maffei, 1971).

There is little need for the visual system to go to the expense of deploying a dual system to separately process *small* luminance perturbations around mean photopic light levels. In such a situation, the relatively low spontaneous firing rate of retinal ganglion cells (e.g. Maffei, 1968) is still effective at signalling both increments and decrements. For instance, if we selectively block the ON-pathway of monkeys by the application of the glutamate neurotransmitter analog 2-amino-4-phosphonobutyrate (APB) then thresholds for increments and decrements of light under photopic conditions are both hardly affected even though only one pathway is still functioning (Merigan & Pasternack, 1983).

However, for larger perturbations from mean light level a single luminance pathway is much more susceptible to neuronal saturation than a dual system (Bayly et al., 1971). Consider a sinusoidual luminance signal whose amplitude is large enough to saturate either or both the luminance pathways (saturate implies that the maximal output of the system has been reached). If there were only one unsigned luminance pathway then the system would simply saturate. However, given the complementary nature of the ON- and OFF-pathways, that one is silent while the other one talks, and given their later convergence on geniculate cells (e.g. Guillery, 1966), then a summation of spatial averages at the level of the geniculate cell (ON-cells forming excitatory (inhibitory) connections and OFF-cells forming inhibitory (excitatory) connections to ON- (OFF-) geniculate cells), would provide distinct advantages in terms of signal to noise ratio and an extension of the linear range of the system before saturation (Bayly et al., 1971). Thus by having two signed luminance pathways the visual system is capable of finer discrimination in the presence of even large perturbations from mean light level. This is achieved at low metabolic cost as there is no need for a high spontaneous firing rate as would be the case if increments/decrements were signalled by the same unitary luminance pathway.

In summary, our experiments have shown that if ON- and OFF-signals are present within a visual scene and offer conflicting percepts then the visual system parses the scene so that the relative activities of the signed luminance pathways are subtracted from each other. This allows the visual system to support finer levels of discrimination than would be possible using only one luminance pathway. Our results suggest that each luminance pathway applies a non-linear, probably logarithmic, compression of its input. Furthermore, by using the two separate pathways in an antagonistic fashion the visual system automatically adapts to the mean light level.

Acknowledgements

Supported by NEI Grant EY 10241-4. Thanks to Kendra Becker, Shannon Downie, Kathy Lau, Paul Jasmeet Singh, Joel Snyder, Matt Soskins, Claudia Spielman, Vernon Stanley, Bethany Taubman, Phyllis Wright and Andrew Daniell for assistance in data collection.

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