Pergamon

0042-6989(95)00164-6

Vision Res., Vol. 36, No. 6, pp. 817–829, 1996

Printed in Great Britain
0042-6989/96 $15.00 + .00

Contrast Discrimination at High Contrasts Reveals the Influence of Local Light Adaptation on Contrast Processing

FREDERICK A. A. KINGDOM,*† PAUL WHITTLE‡

Received 9 November 1994; in revised form 31 May 1995

Previous measurements of contrast discrimination threshold, ΔC, as a function of pedestal contrast, C, for sine-wave gratings have shown a power law relationship between ΔC and C at suprathreshold levels of C. However, these studies have rarely used contrasts greater than 50%. Whittle (1986), using incremental and decremental patches, found that ΔC increased with C only up to about 50%. At higher contrasts it decreased. Since a periodic stimulus can be considered to be composed of increments and decrements, we thought we might find such an inverse U-shaped function for gratings if we used contrasts up to 100%. We tested this for both sine-wave and square-wave stimuli at spatial frequencies from 0.0625 to 8.0 c/deg. We found that for frequencies up to 0.5 c/deg, ΔC in nearly all cases 'dipped down' after about $C = 50\%$ contrast. At 4.0 and 8.0 c/deg, however, no dip-down occurred. Additional experiments showed that the dip-down was unlikely to be due to cortical long-term adaptation and most likely an effect of localized light adaptation to the dark bars. We argue that the absence of dip-down at high spatial frequencies was mainly due to the attenuation of contrast by the optics of the eye. As for the results of Whittle (1986), a Weber's Law in $W = (L_{max} - L_{min})/L_{min}$ describes the inverse U-shaped contrast discrimination function well. Two other contrast expressions also linearize the data on log–log plots. We show how some familiar notions about the physiological operation of localized light adaptation can easily account for the form of the contrast discrimination function. Finally we estimate the number of discriminable steps in contrast from detection threshold to maximum contrast for the various spatial frequencies tested.

Contrast discrimination   Light adaptation   Luminance gain control

INTRODUCTION

In a typical contrast discrimination experiment the subject is required to discriminate between two stimuli that differ in their contrasts: a "pedestal" of contrast C and a "pedestal-plus-increment" of contrast $C + \Delta C$. The minimum value of ΔC which can be reliably detected is known as the contrast discrimination threshold. The relationship between ΔC and C defines the contrast discrimination function and has important implications for the internal processing of contrast. The function is characteristically dipper shaped: as C increases from zero, ΔC first decreases and then increases (Campbell & Kulikowski, 1966; Foley & Legge, 1981; Legge & Kersten, 1983; Ross & Speed, 1991; Foley, 1994). The minimum value of ΔC occurs when C is at around detection threshold. The increase at suprathreshold levels of C is often ascribed to a compressive nonlinearity in the internal response to contrast (Legge & Foley, 1980; Wilson, 1980; Greenlee & Heitger, 1988). Legge, Kersten and Burgess (1987) offered the alternative explanation of a linear contrast response function combined with multiplicative internal noise, and more recently Foley (1994) has suggested that the increase in ΔC with C is due to divisive inhibition. Support for a compressive transducer function for contrast comes also from studies on contrast magnitude estimation (Gottesman, Rubin & Legge, 1981), contrast or brightness scaling (Whittle, 1993) and contrast matching (Swanson, Wilson & Giese, 1984). Our data present a challenge to conventional notions about the rising suprathreshold portion of the contrast discrimination function. We have not attempted to incorporate both the dipper and suprathreshold parts of the function into a single model, since they are believed to be produced by different mechanisms (Georgeson & Georgeson, 1987; Foley, 1994).

Legge (1981) measured ΔC as a function of C for sine-wave gratings and showed that the rising part was well

* McGill Vision Research Unit, Department of Ophthalmology, 687 Pine Avenue West, Montreal, Quebec, Canada H3A 1A1 [*Fax* 514 843 1691].

† To whom all correspondence should be addressed.

‡ Department of Experimental Psychology, Downing Street, Cambridge CB2 3EB, U.K.

fitted by the power law $\Delta C = kC^n$, with the exponent n ranging from about 0.6 to 0.7 depending on spatial frequency. Bradley and Ohzawa (1986) also found a power–law relationship, with exponents from 0.7 to 0.9. Legge and Kersten (1983) measured contrast discrimination with bar stimuli, and found a power–law relationship for both incremental (bright) and decremental (dark) bars, with the exponent averaging about 0.6. All these studies measured ΔC up to pedestal contrasts of only 50%. An earlier and rarely cited study by Kohayakawa (1972) had, however, produced results inconsistent with the monotonic relationship implied by a power–law. Measuring ΔC up to $C = 35\%$ for 2.0 c/deg sine-wave gratings, Kohayakawa found that while thresholds increased up to about 25% contrast, they declined slightly thereafter. A greater decline, though at higher contrasts, was found by Whittle (1986), who used square incremental and decremental test patches to make the first measurements of contrast discrimination over the full range of pedestal contrasts. Whittle described his stimuli in terms of luminance differences ΔL and $\Delta^2 L$, as illustrated in Fig. 1(a and b). When $\Delta^2 L$ was plotted as a function ΔL, a different pattern of contrast discrimination was found for increments and decrements, as illustrated schematically in Fig. 1(d). For increments, $\Delta^2 L$ was proportional to ΔL throughout the suprathreshold contrast range. However, for decrements, $\Delta^2 L$ first increased with ΔL up to about half its maximum value and then progressively decreased as ΔL increased further still. In other words contrast discrimination for decrements, at least when measured in terms of $\Delta^2 L$, improved as the decremental pedestal approached its black limit. The shape of the $\Delta^2 L$ against ΔL function was therefore an inverse U-shape, with poorest contrast discrimination (the peak of the function) occurring when ΔL was about half its maximum value.

A periodic stimulus such as a sine-wave grating can reasonably be considered to consist of both increments and decrements. What might one therefore expect to be the shape of its contrast discrimination function if measured up to full contrast, given the results of Whittle (1986)? The most parsimonious assumption is that the result would be the same in terms of contrast rather than luminance differences. Whittle found that if his increment and decrement data were plotted in terms of Michelson Contrast $C = (L_{\max} - L_{\min})/(L_{\max} + L_{\min})$, instead of $\Delta^2 L$ and ΔL, then the increment and decrement data came together, with ΔC being an inverse U-shaped function of C in the suprathreshold contrast range, as shown in Fig. 1(e). In the present paper we test whether such an inverse U-shaped function occurs for periodic stimuli if measured over the whole suprathreshold contrast range.

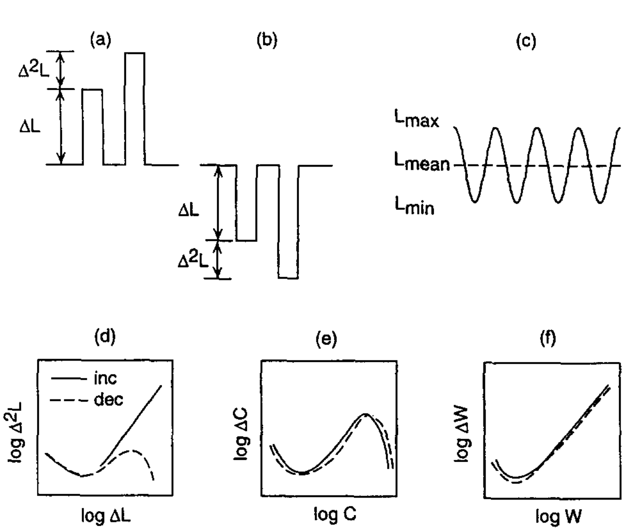

FIGURE 1. Stimulus characteristics and results of Whittle's (1986) study on luminance discrimination using (a) incremental and (b) decremental patches. $\Delta^2 L$ is the minimal discriminable difference in luminance while ΔL is pedestal luminance minus background luminance. (c) Defining characteristics of stimuli used in experiments described here. (d)–(f) Schematic representation of Whittle's results: continuous rule = increment data, dashed rule = decrement data: (d) in terms of luminance differences ΔL; (e) in terms of contrast C where $C = (L_{\max} - L_{\min})/(L_{\max} + L_{\min})$; (f) in terms of W, where $W = (L_{\max} - L_{\min})/L_{\min}$.

METHODS

Apparatus

The stimuli were generated using the VSG2/1 Digital Signal Generator (Cambridge Research Systems) driven by a DELL 386 PC and displayed on a BARCO CDCT 6551 RGB monitor.

Calibration

In any measurement of contrast increment thresholds, it is essential to ensure first that there is sufficient contrast resolution over the whole range, and second that the monitor is properly gamma-corrected. Since we go up to very high contrasts where both the nonlinearity and limited dynamic range of the monitor might make measurements suspect, we report our calibration procedures in some detail.

The VSG2/1 Digital Signal Generator has three 14 bit (16384 levels) DACs (digital-to-analogue converters), one for each RGB channel, which can be mapped onto three 12 bit LUTs (look-up-tables), each thus having 4096 intensity levels. In our experiments all three RGB channels were always set to the same DAC value, thus producing only black–white stimuli. Our calibration procedures therefore effectively deal with a single monochromatic monitor gamma. We first measured, with a UDT photometer, the luminance of the central bar of a 0.05 c/cm square-wave (like one of our experimental stimuli), produced with an approximately linearized LUT at 5% contrast intervals between −100% (when the central bar was dark) to +100% (central bar bright). Using these measurements we then generated, and checked, a precisely linearized LUT. This defined which DAC values (1–16384) were associated with each of the 4096 intensity levels available for the monitor.

After checking that the LUT was linear for a set of coarsely sampled contrasts throughout the contrast range, we went on to measure the luminance of both bright and

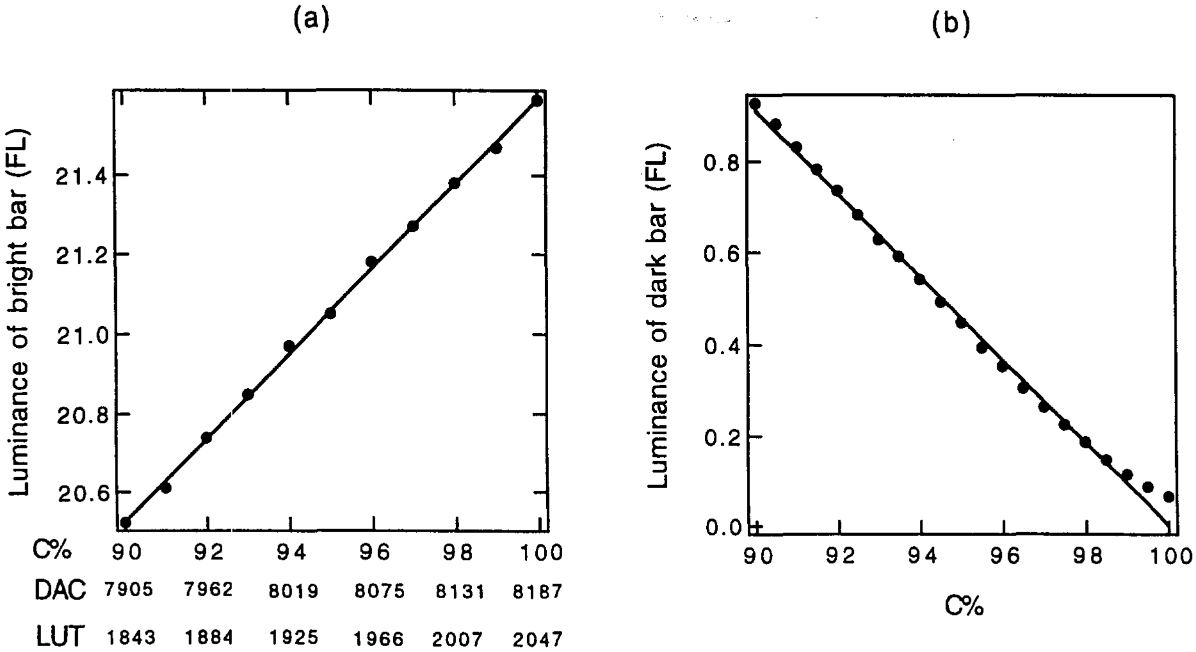

FIGURE 2. Luminance measurements of the bars of a square-wave grating between 90 and 100% contrast. (a) Dark bar; (b) bright bar. In (a) the DAC (digital-to-analogue) values and LUT (look-up-table) values are also shown on the abscissa.

dark bars of the square-wave grating at 1% intervals between nominal 90 and 100% contrasts. We made three luminance measurements at each contrast in random order presentation, and also noted their associated LUT and DAC values. For the bright bar this established whether there was sufficient luminance resolution in the steepest part of the monitor gamma. For the dark bar this provided an estimate of the minimum luminance of a nominally 100% contrast stimulus, and checked the linearity of the LUT in the flattest part of the gamma. The results are shown in Fig. 2 which plots the mean luminances of the bright [Fig. 2(a)] and dark [Fig. 2(b)] bars as a function of their nominal contrast. For the bright bar [Fig. 2(a)] LUT values and DAC values are also shown on the abscissa. It can be seen that the luminances of both bright and dark bars are nearly linear functions of nominal bar contrast up to about 98.5%, where the minimum luminance of the dark bar sets an upper limit to contrast. For the bright bar [Fig. 1(a)] the DAC resolution is greater than that of the LUT resolution all the way up to maximum contrast. At its lowest, the DAC:LUT ratio is 1.4 between $C = 98$ and 100% for the bright bar. This means that no two adjacent LUT values will be associated with the same DAC value, and there are enough DAC values between adjacent LUT values to continue to generate almost constant increments in luminance at the high end of the range.

In summary, the measurements show that from 0 to 98.5% contrast there are 2017 (less than 2048 because of the cut-off at 98.5%) distinct levels of contrast at virtually identical contrast intervals, providing a contrast resolution of 0.05% throughout the contrast range. This value is about a factor of three smaller than the smallest contrast increment threshold measured in the experiments described below.

Even though the contrast resolution of our stimuli is sufficient it is possible that higher harmonic distortions exist in the high contrast sine-wave stimuli. To check the fidelity of the high contrast sine-waves, we measured the luminance profile of a nominally 100% contrast sine-wave whose spatial frequency was 0.0078 cycles per raster line, or 0.25 c/deg in the experiments. For this we used a Hagner Universal Microphotometer (Opticon) with its circular aperture focused onto an area approx. 4 pixels (raster lines) in diameter, or 1/32 of the sine-wave cycle, by the addition of suitable lenses. The region outside the field of view of the aperture was occluded with black card to minimize the effects of surrounding light scatter. Measurements were made at 36 phase positions of the sine-wave. The results are shown as the solid circles in Fig. 3, with the continuous line an actual sine-wave fitted to the data. As the figure shows there are no visible distortions in the sine waveform.

Stimuli

We employed both sine- and square-wave stimuli. They were presented in a circular hard edged window on a background set to the same mean luminance as the grating, which was 37.0 c/deg m^2. Four cycles of the test gratings were displayed in the window. In the 0.0625 c/deg condition only one cycle was displayed and the stimulus was not windowed. The stimuli were all presented with a linear ramp at both onset and offset of 1/4 of the total stimulus presentation time, implying that they were at full contrast for 1/2 the total presentation time. In the standard condition total presentation time was 0.4 sec. We used a range of pedestal contrasts from 0.0 to 98.5%: 0.0, 1.25, 2.5, 5.0, 10.0, 20.0, 40.0, 50.0, 60.0, 70.0, 80.0, 90.0 and 98.5%. These are logarithmically spaced up to 40% as in previous studies, but

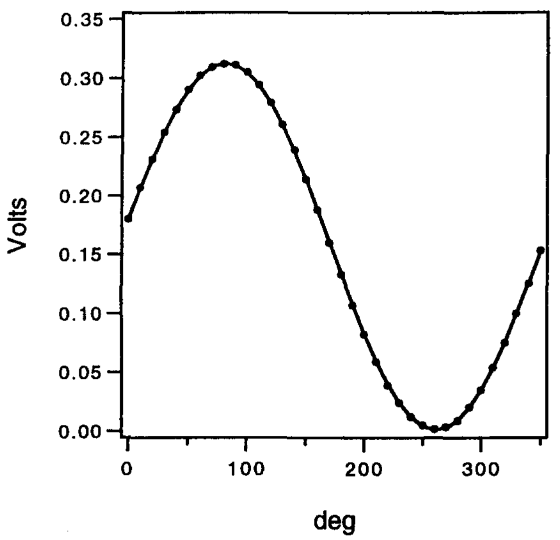

FIGURE 3. Luminance profile of the 0.25 c/deg sine-wave at nominally 100% contrast, measured as the voltage output of a microphotometer. The physical spatial frequency of the sine-wave was 0.0078 c/raster line, and the circular aperture of the photometer was focused onto an area approx. 4 raster lines in diameter, or 1/32 of a cycle. The solid circles show the voltage measurements, while the continuous line shows a sine-wave fitted to the data.

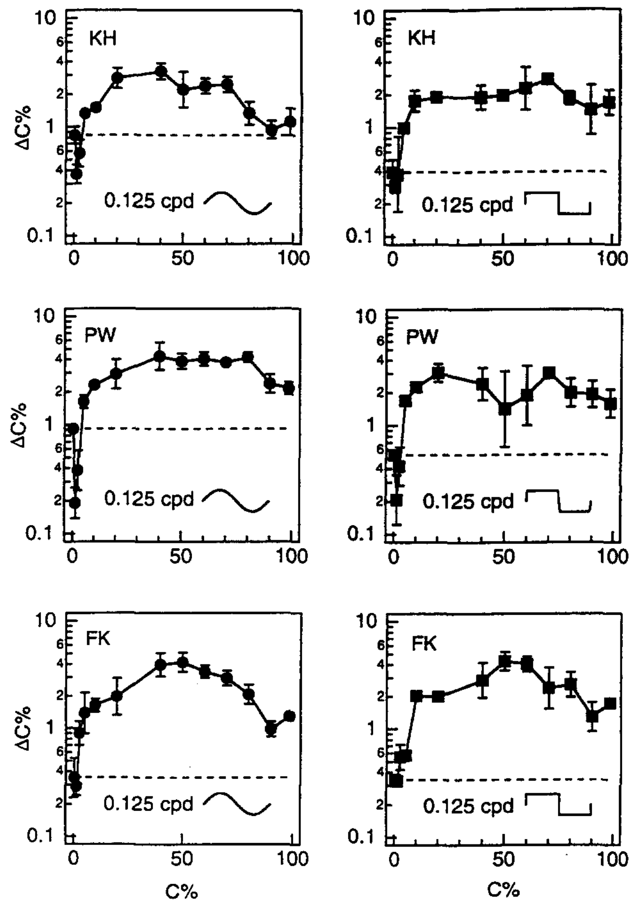

FIGURE 4. Contrast discrimination functions for the 0.125 c/deg condition. Symbols next to 0.125 c/deg label indicate whether the stimulus was a sine-wave or a square-wave. Note that ΔC is on a log axis whereas C is on a linear axis. The dashed rule is a continuation of the first contrast threshold data point. Results are shown for three subjects.

linearly spaced above 40% to enable a detailed examination of contrast discrimination performance at high pedestal contrasts. We measured performance at spatial frequencies of 0.0625, 0.125, 0.5, 4.0 and 8.0 c/deg. For the 0.0625, 0.125 and 0.5 c/deg stimuli, viewing distance was 73.5 cm. The 4.0 and 8.0 c/deg conditions used identical stimuli as the 0.5 c/deg stimulus but viewed at 588 and 1176 cm, respectively. This was to ensure that any changes in the shapes of the contrast discrimination functions at these higher spatial frequencies could not be due to the attenuation characteristics of the monitor. The phase of the gratings was fixed in sine-phase at the centre of the window, except in those experiments that specifically studied the effects of phase.

Procedure

A 2IFC (two interval forced choice) procedure was used to measure ΔC. In the standard condition the interval between the two stimuli of each forced-choice pair was 1.0 sec. The subject had to decide in which interval the stimulus, C or $C + \Delta C$, had the greatest contrast and a button press recorded their decision. It also initiated the next trial, which began after an interval of 1.0 sec. A standard "two-up, one-down" staircase procedure was used to measure the threshold ΔC (Levitt, 1971), which gives a value corresponding to 70.7% correct detections. When the staircase required a change in ΔC it was either incremented or decremented by a fixed ratio of 1.5. The first two reversals of the staircase were ignored and the session was terminated after 10 additional reversals. The threshold value of ΔC was calculated as the *geometric* average of ΔC over those 10 reversals. For pedestal contrasts less than 50% the procedure established the contrast *increment* threshold, whereas above 50% it established a *decrement* threshold. This was necessary to prevent the combination of C and ΔC ever falling outside the range of 0–98.5%. In any one experimental session staircases at different pedestal contrasts were run in a random order.

Subjects

Five subjects participated in this experiment, the two authors FK and PW and three naive subjects, KH, SB and VT who were paid volunteer research assistants at McGill University. All had normal or corrected-to-normal visual acuity. Not all subjects completed every condition.

RESULTS

Figures 4–7 present the results for the 0.125, 0.5, 4.0 and 8.0 c/deg conditions, respectively. Note first that the data are plotted on log–linear, rather than log–log, plots in order to show ΔC in detail at high pedestal contrasts. This has the effect of squashing the "dipper function" in ΔC seen at very low C up against the left hand side of each graph. Each data point is the geometric mean of three or four thresholds and the bars represent standard errors. Although data points below $C = 50\%$ were contrast increment thresholds, whereas data points above $C = 50\%$ were contrast decrement thresholds, they are

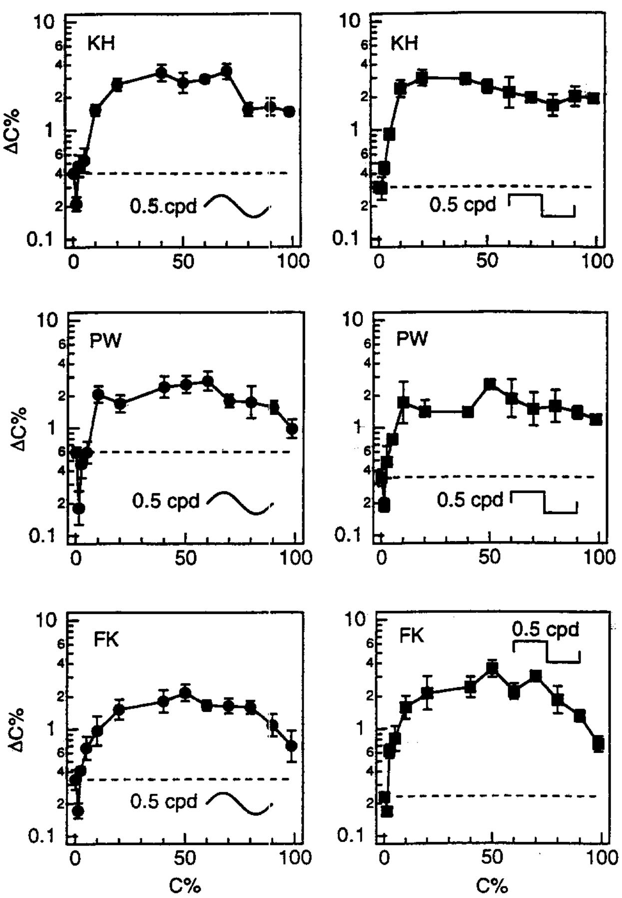

FIGURE 5. Results for the 0.5 c/deg condition for three subjects.

given the same symbols on the assumption that for small ΔC there will be negligible differences depending on whether the standard is larger or smaller in contrast than the test. Inspection of the graphs show that the data appear to fall into roughly two groups, depending on spatial frequency. For the 0.125 and 0.5 c/deg stimuli (Figs 4 and 5) the contrast discrimination function has varying degrees of an inverse U-shape, with ΔC diminishing at values of C above about 50%. For the 4.0 and 8.0 c/deg stimuli (Figs 6 and 7), however, no such inverse U-shaped function is observed. To obtain a clearer picture of the extent of the U-shape in the functions we fitted a quadratic polynomial to the log ΔC values between $C = 1.25$ and 98.5%. We then took the second derivative of the fitted function as a measure of its curvature. The results are shown in Fig. 8. The sign of the second derivative has been inverted so that a high positive value reflects a high degree of negative curvature, or a pronounced inverse U-shape. The overall trend in the data is clearly towards a reduction in the extent of the inverse U-shape as spatial frequency increases, though there is little consistent change across subjects between the 0.125 and 0.5 c/deg conditions.

The mechanisms for improved contrast discrimination at high contrasts

We now consider two possible reasons for the "dip-down" in ΔC at high pedestal contrasts that occurred in the 0.125 and 0.5 c/deg conditions.

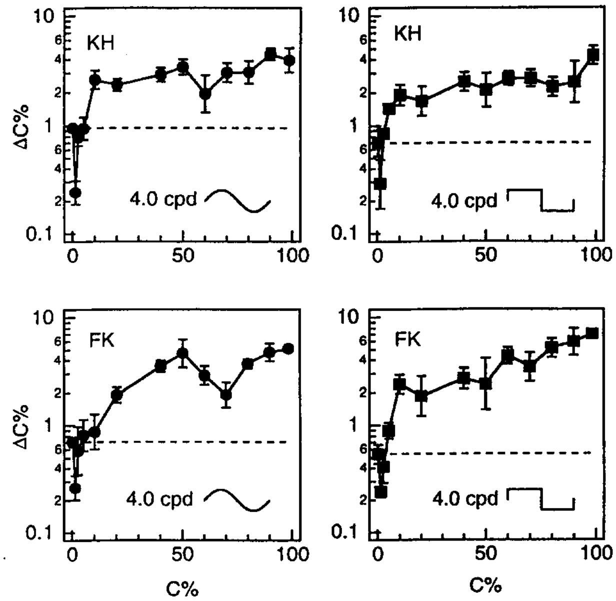

FIGURE 6. Results for the 4.0 c/deg condition for two subjects.

(1) Cortical adaptation? One explanation for the dip-down is the operation of cortical long-term adaptation mechanisms. It is well known that prolonged inspection of high contrast gratings elevates detection thresholds for subsequently presented test gratings (Blakemore & Campbell, 1969) and reduces their apparent contrast (Blakemore, Muncey & Ridley, 1973). More recently Greenlee and Heitger (1988) have provided some evidence that adaptation to high contrast gratings ($C > 50\%$) can in addition improve contrast discrimination thresholds at high pedestal contrasts. They found that ΔC at $C = 80\%$ was reduced by a factor of about two after 5 min adaptation. Although this result has not been replicated (Ross & Speed, 1991), and although it is unlikely that the stimuli we employed were exposed for long enough in our test runs to produce such an effect, we nevertheless have investigated this possibility. We compared ΔC at two inter-trial intervals (ITIs) of 1.0 sec (the standard condition) and 6.0 sec. We reasoned that 6.0 sec ITI would prevent any significant build-up of adaptation during a session and so would remove the dip-down at high C if the long-term adaptation hypothesis was true. ΔC was measured at $C = 5$, 50 and 95% for both sine-wave and square-wave stimuli and the results are shown in Fig. 9. In three out of four cases the dip-down in ΔC is preserved in the 6.0 sec condition, though it appears to be reduced in overall magnitude in all conditions. The reduction in the overall magnitude of the dip-down is principally caused by a reduction in ΔC for the 50% condition at the 6.0 sec ITI, and we are unable to offer any explanation for this effect. We conclude, however, that if long-term adaptation is having an effect, it is having a very small one and that it is not the principal cause of the dip-down in ΔC at high pedestal contrasts that we have observed.

(2) Local retinal light adaptation? A second possible cause of the dip-down in ΔC at high C is local light adaptation within the stimuli. (We use the generic term

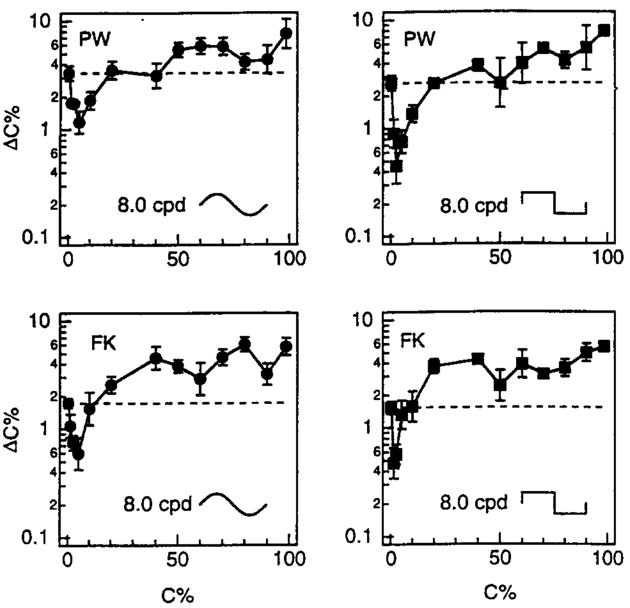

FIGURE 7. Results for the 8.0 c/deg condition for two subjects.

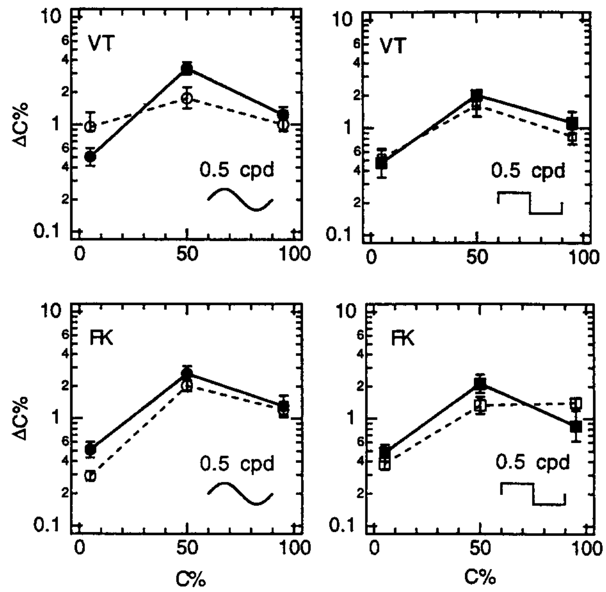

FIGURE 9. Effect of inter-stimulus interval (ITI) on ΔC at $C = 5$, 50 and 95%. Solid rules = ITI of 1.0 sec; dashed rules = ITI of 6.0 sec.

light adaptation for adaptation to a change in luminance, although it is probably strictly speaking dark adaptation, adaptation to a decrease in luminance, that is more important here.) This could produce the dip-down either by compressing the intensity-response function prior to contrast processing, or if the contrast processing mechanisms themselves locally adapted to the dark bars. We discuss these two possibilities in more detail later on. Adaptation is very fast at photopic levels. When luminance is reduced, the increment threshold for a brief probe flash falls rapidly for the first 150 msec or so, levelling out between 150 and 250 msec (e.g. Crawford, 1947). If the dip-down is due to local adaptation we would therefore expect it to be reduced at stimulus exposures significantly less than 150 msec. Figure 10 shows results for exposure durations of 0.125, 0.35 and 1.0 sec. Note that these durations should be halved to obtain the time for which the stimulus was on at full contrast because of the linear ramp at onset and offset. We see that the dip-down occurs at both 0.35 and 1.0 sec but not at 0.125 sec, except for a slight effect in VT's sine-wave data. These results are therefore largely consistent with the known dynamics of early light adaptation and thus support the hypothesis that the dip-down is caused by such adaptation.

Effect of phase

In all the experiments described so far the stimuli were presented in sine phase, that is with a dark and a bright bar on either side of the center. Fixation was free and some subjects said that they fixated on the dark bar in order to maximize their performance. Is foveal fixation of the dark bar essential to produce the dip-down? To answer this we measured ΔC for 0.5 c/deg gratings in both fixed- and random-phase presentations, requiring subjects to maintain fixation on a tiny dot in the middle of the screen. The results in Fig. 11 show no consistent differences between fixed and random phase conditions. Therefore, at least for 0.5 c/deg gratings, the dip-down is not restricted to the particular phase conditions used in the other experiments, and fixation directly on the dark bar is not necessary. To test the generality of this conclusion at frequencies low enough for a half cycle to

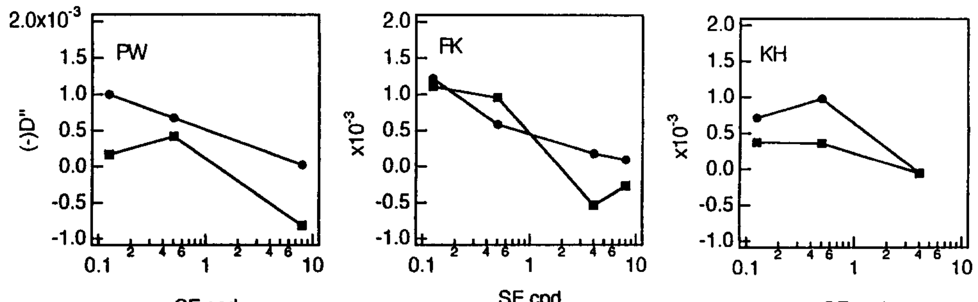

FIGURE 8. The magnitude of the dip-down in ΔC is shown as a function of spatial frequency for three subjects. The ordinate gives ($-$) the value of the second derivative of the best fitting quadratic function to the data. The second derivative is an estimate of the curvature of the contrast discrimination function. Values greater than zero indicate a dip-down in ΔC while values less than zero indicate no dip-down.

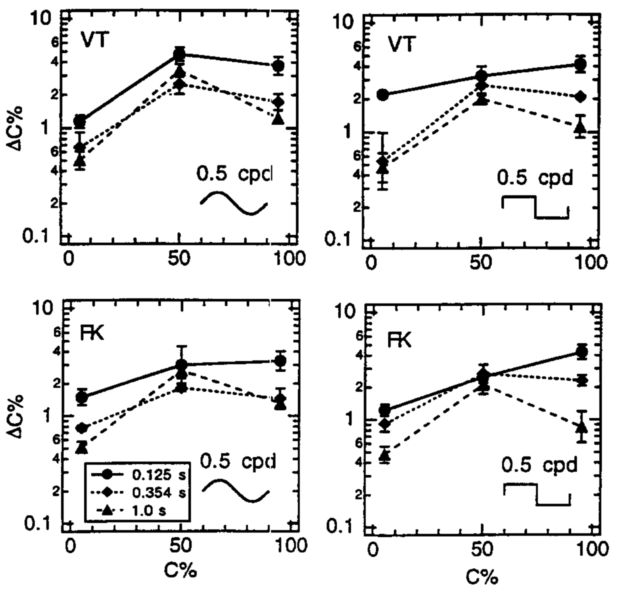

FIGURE 10. Effect of stimulus exposure duration for $C = 5$, 50 and 95%. Exposure times are given in FKs sine-wave graph.

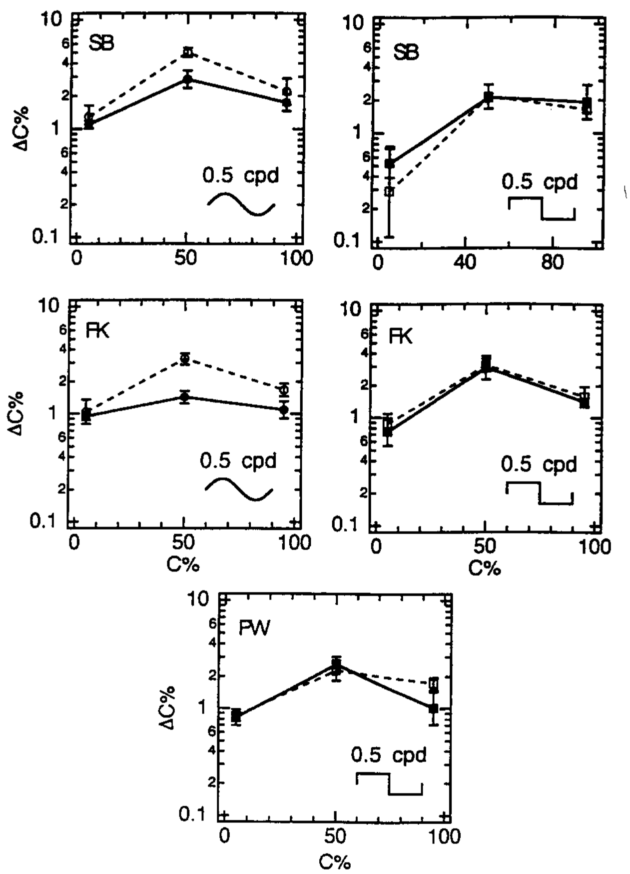

FIGURE 11. Effect of phase randomization for $C = 5$, 50 and 95%. Solid rules = fixed phase; dashed rules = random phase.

occupy a significant part of central vision, we went on to measure ΔC for a 0.0625 c/deg stimulus, for which one cycle filled the entire screen. The stimuli were presented in fixed phase, centred on either the dark or the bright bar. The results are shown in Fig. 12. For both subjects a large dip-down occurred for all dark-bar-centred stimuli (solid symbols), as expected. For the bright-bar-centred stimuli (open symbols) on the other hand, there was no dip-down in three out of four conditions and only a slight one in the fourth (KH, square-wave). Therefore, the dark bar does seem to be salient for contrast discrimination in this rather extreme case where each bar is 8 deg wide.

This is somewhat puzzling, particularly for square-wave stimuli. Since the edge is in the same place irrespective of whether the dark or bright bar is central, it cannot in this case be the mechanisms acting at the edge that are critical for accurate contrast discrimination. It suggests instead that the critical feature here is the accurate registration of the luminance of the dark bar.

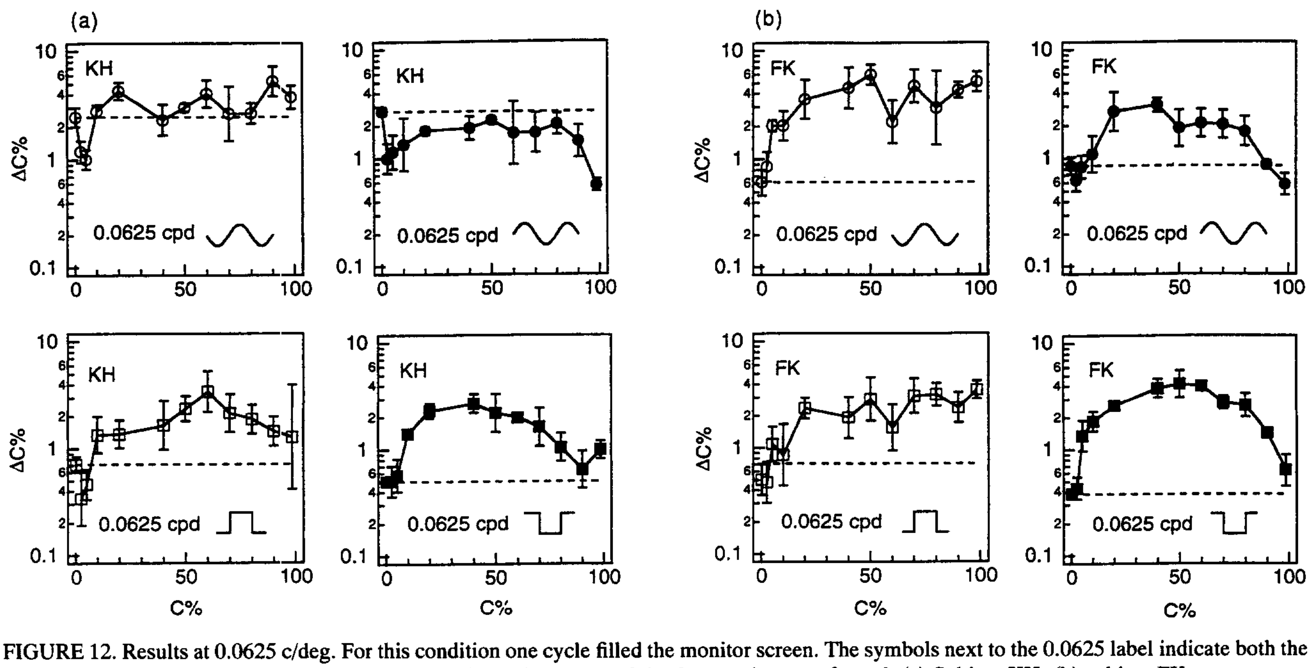

FIGURE 12. Results at 0.0625 c/deg. For this condition one cycle filled the monitor screen. The symbols next to the 0.0625 label indicate both the type and phase of the stimuli, and indicate the nature of the feature that was fixated. (a) Subject KH; (b) subject FK.

TABLE 1

			Power law in W			Power law in C		
S	c/deg	Stimuli	k	n	R^2%	R^2%	n ($C < 50\%$)	N
FK	0.125	Sine	0.19	0.96	98.1	66.9	0.63	51
FK	0.125	Square	0.17	1.02	98.4	81.8	0.68	54
KH	0.125	Sine	0.16	0.93	97.6	62.3	0.55	58
KH	0.125	Square	0.15	1.01	97.8	86.0	0.54	64
PW	0.125	Sine	0.21	1.07	99.1	86.0	0.82	41
PW	0.125	Square	0.16	1.00	97.1	74.4	0.58	64
FK	0.5	Sine	0.11	1.01	98.6	79.7	0.66	86
FK	0.5	Square	0.15	1.00	98.9	72.1	0.73	68
KH	0.5	Sine	0.15	1.05	98.8	83.7	0.83	61
KH	0.5	Square	0.17	1.00	97.6	80.7	0.75	57
PW	0.5	Sine	0.14	1.03	98.6	79.8	0.75	66
PW	0.5	Square	0.13	1.01	97.6	81.7	0.57	76
FK	4.0	Sine	0.18	1.11	98.1	95.4	0.72	49
FK	4.0	Square	0.20	1.13	98.5	96.4	0.65	46
KH	4.0	Sine	0.20	1.05	97.7	91.1	0.64	43
KH	4.0	Square	0.18	1.01	97.0	90.1	0.47	49
FK	8.0	Sine	0.17	1.21	99.2	91.1	0.83	40
FK	8.0	Square	0.23	1.04	97.9	94.5	0.57	36
PW	8.0	Sine	0.22	1.15	99.0	92.2	0.58	28
PW	8.0	Square	0.19	1.18	99.0	97.5	0.67	37

All parameters are calculated over the full range of suprathreshold pedestal contrasts up to 98.5%, except where specified as $C < 50\%$. S, subjects; K, constant; n, exponent; R^2, proportion of the total variance accounted for by the linear fit; N, number of discriminable steps.

This supports the conclusion of the previous section, that local adaptation is important, but it also leaves a puzzle as to why local luminance is more accurately perceived in the central than in peripheral retina.

DISCUSSION

The principle finding of this study is that the traditional description of contrast discrimination in terms of a power law in C is not applicable when ΔC is measured throughout the contrast range, if the stimuli are of low to medium spatial frequency and presented for about 200 msec or longer. Whereas a power law predicts that ΔC should monotonically increase with C, we find that it reaches a maximum at about 50% contrast and then decreases to a greater or lesser extent as C approaches its upper limit. That is, contrast discrimination *improves* as contrast increases in the high contrast range. We suggest that this improvement is due to the influence of local light adaptation on contrast processing. The main evidence for this was that the dip-down in ΔC at high C disappeared at exposure durations of less than about 150 msec. One other possible cause of the dip-down was considered but rejected. We found that increasing the inter-trial interval from 1.0 to 6.0 sec neither worsened contrast discrimination at 90% pedestal contrast, nor eliminated the dip-down, thus making it unlikely that the effects were due to long-term cortical adaptation.

Comparison with previous studies

The only study known to us to have shown a dip-down in ΔC in the suprathreshold range of contrasts using periodic stimuli is by Kohayakawa (1972), who measured ΔC up to $C = 35\%$ with 2.0 c/deg sine-wave gratings. He found that ΔC decreased after about $C = 25\%$. In our data, however, the decrease does not occur until at least $C = 50\%$. Given the numerous studies which have measured ΔC up to $C = 50\%$, none of which have found a dip-down, Kohayakawa's result must be seen as anomalous. Two features of his study differed from current practice. The stimuli were presented in an optical system rather than on a CRT, and the gratings to be discriminated were spatially abutting. It would be interesting to try to replicate his measurements using a computer monitor, to see if contiguous gratings produced a dip-down at lower contrasts than we found. The only study we are aware of which measured ΔC in the high contrast range is that by Greenlee and Heitger (1987) who went up to 80% pedestal contrast. Their measurements without prior adaptation, the condition comparable to ours, show no hint of a dip-down. One possible reason is their choice of spatial frequency: 2.0 c/deg. This falls in the gap between our 0.5 and 4.0 c/deg measurements, so it is possible that we also would have found no dip-down at 2.0 c/deg, as was the case at 4.0 and 8.0 c/deg. It is worth noting, however, that their plots of ΔC against C show a more or less linear relationship between ΔC and C throughout the contrast range. This is at odds with all previous reports, which have shown ΔC to be a power function of C with an exponent substantially less than 1.0, including Legge's (1981) study which found an exponent of 0.6 for 2.0 c/deg gratings. Such a power law would be a negatively accelerated curve on the linear plots used by Greenlee and Heitger, whereas their data show, if

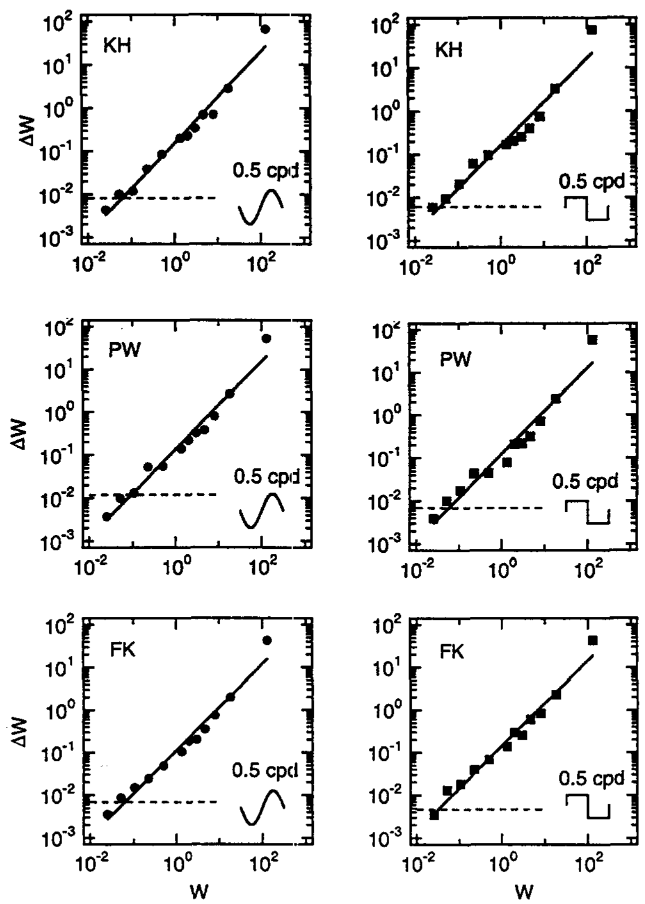

FIGURE 13. Results of the 0.5 c/deg condition plotted in terms of W, where $W = (L_{max} - L_{min})/L_{min}$. Note that the data are now plotted on log–log axes. The straight lines are the best fitting linear fits to the log-transformed data for the rising part of the contrast discrimination function.

anything, a slight positive acceleration. There may therefore have been other features of their procedure which made their results differ both from most previous studies and from ours.

To compare our results with the often quoted study by Legge (1981), Table 1 gives the values of the exponent n for the best fitting power law in C for our data points over the restricted contrast range from 1.25 to 50.0%, which was the maximum used by Legge. He found average exponents of 0.6 at 2 c/deg and 0.7 at 8.0 c/deg, which are similar to our average exponents of 0.63, 0.72, 0.62 and 0.66 for the 0.125, 0.5, 4.0 and 8.0 c/deg conditions, respectively. We now consider how our results with periodic stimuli compared to those of Whittle (1986).

The metric W

In the Introduction we described the results of Whittle's (1986) study which measured contrast discrimination thresholds for both incremental and decremental test patches. Although the results for increments and decrements were very different at high contrasts when plotted in terms of luminance differences (see Introduction), they came together when plotted in terms of the contrast expression $W = (L_{max} - L_{min})/L_{min}$, and were well described by the power law $\Delta W = kW^n$. The exponent n was close to unity, implying a Weber's Law in W. This is shown diagrammatically in Fig. 1(f). The same relation describes our results with gratings. Figure 13 shows our data for 0.5 c/deg stimuli with contrast expressed as W rather than C. Each log–log plot shows the best linear fit to the rising portion of the curve. As can be seen, these linear fits are very good. Table 1 gives the best fitting values of k and n. n is always close to unity for the spatial frequencies 0.125 and 0.5 c/deg, showing that our results with periodic stimuli are very similar to those for Whittle's patch stimuli. The superiority of the power law in W over the traditional power law in C as a description of contrast discrimination over the full contrast range, is also forcefully shown by the goodness-of-fit measures in Table 1. R^2, the proportion of the total variance accounted for by the linear fit, is obviously much larger for the former, particularly for the 0.125 and 0.5 c/deg data. A power law in W also describes the higher frequency data, at 4.0 and 8.0 c/deg, but the exponent is then somewhat more than 1.0.

The fact that a Weber's Law in W gives such a good description of data for increments, decrements and sine and square wave gratings, points to a common mechanism for contrast discrimination of all these stimuli. Although we have only measured contrast discrimination at one mean luminance, we assume we would obtain similar findings at other mean luminances on the basis of previous studies. Whittle (1986) found that a power law in W fitted his increment and decrement data over a range of mean luminances from 1.35 to 4.35 log td when normalized with respect to detection threshold. Jamar and Koenderink (1984) found that the detection of contrast modulation in sine-wave gratings was independent of mean luminance as measured in the range 0.02–90 td, even though simple detection thresholds showed the classic de Vries-Rose square-root dependence on mean luminance.

The functional significance of W, L_{min} *and* C

The denominator of contrast expressions like C and W can be interpreted as a divisive gain parameter set by light adaptation. Therefore, the first hypothesis suggested by the power law in W is that the contrast-processing mechanisms locally adapt to L_{min}, at least at low spatial and temporal frequencies, so that $1/L_{min}$ is the gain factor for the mechanisms that detect ΔL. C uses L_{mean} in the denominator. At low contrasts the ratio $L_{mean}:L_{min}$ is close to unity but at high contrasts it becomes large. Hence the positive acceleration of W with respect to C. In functional terms, if L_{min} is the right gain parameter, L_{mean} overestimates it at high contrasts so C underestimates the visually effective contrast. Hence the dip-down in ΔC at high contrasts.

The unsatisfactory nature of C in representing contrast discrimination could be seen clearly in Whittle (1986). He found a marked dip-down in discrimination thresholds for decrements, but not for increments, when the data were plotted as $\Delta^2 L$ vs ΔL. But this important difference was obscured when the data were plotted in terms of ΔC vs C (see Fig. 1). Both increments and decrements then showed a dip-down because the C metric compressed the high contrasts for both of them. Note, incidentally, that this also implies that a dip-down in C, as in the present data, is not a good basis from which to deduce the underlying visual processes. One should not infer, for example, that $L_{\min}$ must physically decrease over the contrast range used: Whittle's data showed just as big a dip-down in C for increments, for which $L_{\min}$ was constant.

What might be the physiological correlate of a power law in W? While it is not our intention to consider in detail how our data might be explained by current models of light adaptation, some elementary and familiar notions about light adaptation nevertheless suffice. The central idea is that light adaptation is rapid and highly localized. There is good psychophysical evidence that at photopic levels adaptation may be localized to within the diameter of a cone (Burr, Ross & Morrone, 1985; Macleod, Williams & Makous, 1992), and neurophysiological evidence from the cat suggests that it is at least localized to within the receptive field center of ganglion cells (Shapley & Enroth-Cugell, 1984). This high degree of localization explains how $L_{\min}$ could be the gain parameter of a retinal mechanism which processes contrast, such as a ganglion cell, even when, as in the sine-wave condition, $L_{\min}$ is restricted to a thin strip. An "OFF" center ganglion cell, whose response to contrast was divided by the mean luminance sampled over its receptive field centre, would give its biggest response when its receptive field was centered on $L_{\min}$, the darkest part of the stimulus. If we assume that the responses of such cells are also compressively transformed (either directly, or more likely at a later cortical stage where the outputs of "ON" and "OFF" retinal cells are combined for contrast processing) then the result is the necessary contrast-response function for producing a power law in W for contrast discrimination (see Appendix for details).

Although a number of previous models have combined light adaptation and contrast processing (e.g. Hayhoe, Benimoff & Hood, 1987; Bowen & Wilson, 1994), none have used $L_{\min}$ as the gain parameter. For example, Burr *et al.* (1985), in commenting on psychophysical results that implied highly localized light adaptation, state on p. 726 "For single objects contrast is usually $(L_o - L_b)/L_b$, where L_o is the luminance of the object and L_b the luminance of the background . . . If gain control is as local as the present experiments suggest, mean or background luminance is not the most appropriate normalization factor. . . Our results suggest that a more appropriate definition . . . may be $(L_o - L_b)/L_o$ so that the luminance which sets the local gain, L_o, is also the denominator for contrast". The results here, however, suggest that if one adopts a model which combines contrast processing with localized divisive gain control, the denominator should be $L_{\min}$ rather than L_o. L_o will in fact be the divisor everywhere, but discrimination thresholds will depend on the regions where the signals from the two gratings differ most, and we suggest that those regions are where L_o is minimum.

Alternatives to W

Kingdom and Moulden (1991) re-analysed Whittle's (1986) increment and decrement contrast discrimination data using the metric $G = \ln(L_{\max}/L_{\min})$, and found that a power law in G, namely $\Delta G = kG^n$, with the exponent $n = 0.69$, linearized the data on a log–log plot. At the time Kingdom and Moulden argued that W, which Whittle had employed, was not a physiologically realistic measure of contrast because the gain parameter that it suggests, $L_{\min}$, was the background luminance for increments and the test patch luminance for decrements. Surely, they argued, it need not be different for the two classes of stimuli. In the light of our suggestions above on how W could be realized physiologically, their argument now appears ill conceived. However, G remains an attractively simple contrast expression, and it is of some interest that a power–law in G also linearizes the data here well, though not as well as W. The mean R^2 value for the 0.5 c/deg data is 95%, compared to W which gives a better fit of 98%. The average exponent for the power law in G is 0.74. Interestingly, Legge and Kersten (1983) have also argued for the log transform, as part of the explanation for why Michelson C brought together their incremental and decremental bar contrast discrimination functions. Legge and Kersten showed that C was approximately equal to $\log(L_o/L_b)$ up to about $C = 0.7$. C worked, they argued, because it reflected the logarithmic response of retinal neurones to intensity. The irony is that had they measured bar contrast discrimination up to maximum contrast, as Whittle (1986) did, they would almost certainly have found that the logarithmic transform gave a *better* fit to their data than C, precisely because $\log(L_o/L_b)$ works better than C in the high contrast range where the two metrics differ.

Another function that is used almost as often as the logarithm to describe an early non-linearity is the Naka–Rushton equation $R(I) = R_{\max}L/(L + s)$ where $R_{\max}$ is the maximum possible response, L luminance and s the semi-saturation constant (Naka & Rushton, 1966). To derive an expression for contrast, we apply the Naka–Rushton equation to $L_{\max}$ and $L_{\min}$ separately (putting $R_{\max} = 1$) and then define Z as the difference between the two. This gives $Z = L_{\max}/(L_{\max} + s) - L_{\min}/(L_{\min} + s)$. Z shares some properties with W and G [in fact $R(I)$ is approximately proportional to the logarithm for suitable choice of s, so that then Z is approximately proportional to G]. The linear fits for a power law in Z are quite excellent. The mean R^2 value for the 0.5 c/deg data with s set to 0.17 of L_{mean} is 98.4%, which is fractionally superior to the fit obtained with W. The average exponent of the power law in Z for the 0.5 c/deg data is 0.76.

W, G and Z all linearize the data because they are positively accelerated functions of C, as illustrated in Fig. 14. The more positively accelerated, the higher the exponent of the corresponding power law. Conversely, C is a negatively accelerated function of W, G and Z:

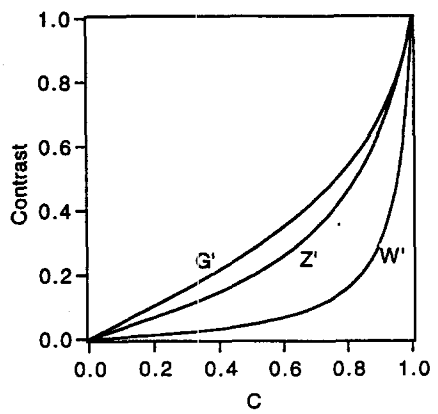

FIGURE 14. Contrast functions W, G and Z plotted against C. $W = (L_{max} - L_{min})/(L_{min} + L_0)$; $G = Ln(L_{max} + K)/(L_{min} + L_0)$; $Z = (L_{max}/(L_{max} + L_0 + s)) - (L_{min}/(L_{min} + L_0 + s))$. $L_0 = L_{mean}/20$, $s = 0.17L_{mean}$. The quantities plotted are normalized values $W' = W/W_{max}$, $G' = G/G_{max}$, $Z' = Z/Z_{max}$ where W_{max}, G_{max} and Z_{max} are the values of W, G and Z when $C = 1.0$.

relative to them it expands the low end of the contrast range and compresses the high end. If a Weber's law in W describes contrast discrimination, the dip-down in C follows mathematically from the nature of the C metric. Note that it is not the restriction of C to the interval 0–1 that is the problem. Z is similarly restricted, and any metric can be constrained to this interval by normalizing by some maximum value, as has been done for W and G in Fig. 14. That simply scales the axes without affecting characteristics like the inverse U-shape of the discrimination functions.

Physiologically, power–laws in G and Z suggest a more-or-less pointwise, compressive non-linear transform of the luminance profile before contrast is processed, as assumed in a recent study on masking by Bowen and Wilson (1994). This compressive non-linearity corresponds to the logarithmic (in G) or Naka–Rushton (in Z) transform, and has the effect of enhancing the contrast of the dark relative to the bright bars, especially at high contrasts. This scheme differs from the one suggested above for W, in that here there is compression before contrast is computed, whereas the model for W proposed a single stage of light adaptation plus contrast processing. In both cases the output of the contrast processing stage would be subject to a further compressive non-linearity.

Sine-wave vs square-wave stimuli

One prominent feature of our data is that in not one single measure of contrast discrimination have we found any significant differences between sine- and square-wave stimuli. This is perhaps not surprising at high spatial frequencies since the higher harmonic components in the square-wave will then be so attenuated as to contribute little in terms of their contrast energy. However, this is not the case at low frequencies. The simplest explanation for the lack of difference between sine- and square-wave stimuli is that contrast discrimination performance is indeed dependent on only two stimulus parameters: L_{max} and L_{min}. This in turn is consistent with the view that the multiplicative light adaptation processes which we have argued are responsible for the dip-down in ΔC, are indeed set very locally, since L_{min}, spatially half a cycle in a square-wave, is localized to a point in a sine-wave.

Why is there no dip-down in ΔC at high C for the 4.0 and 8.0 c/deg conditions?

We find no improvement in ΔC at high C for the 4.0 and 8.0 c/deg conditions. A trivial consequence of this is that a power law in C fits these data quite adequately, as shown by the R^2 values in Table 1. Two likely reasons for the lack of a dip-down in ΔC in the 4.0 and 8.0 c/deg conditions are: (a) attenuation of contrast by the optics of the eye; and (b) adaptational pooling. The effect of attenuation will be to shift the curve relating ΔC to C along the C-axis and if large enough will prevent the dip-down in ΔC. To estimate the effect on our 4.0 and 8.0 c/deg gratings we used the measurements of contrast attenuation provided by Campbell and Gubisch (1966) for a pupil size of 3.8 mm, which was approximately the measured pupil size of FK during the experiments. The mean value of attenuation, defined here as the proportion of contrast remaining, across the three subjects in Fig. 7 of Campbell and Gubisch was 74% at 4.0 c/deg and 51% at 8.0. This degree of attenuation is certainly enough to eliminate the dip-down in ΔC at 8.0 c/deg and substantially reduce it at 4.0.

A second possibility under the power law in W description is that L_{min} is not the divisive gain factor of the mechanisms that encode contrast at 4.0 and 8.0 c/deg, as we argued it was at lower frequencies. In the limit it is of course implausible that the factor is exactly L_{min}, since W would become infinity at maximum contrast. A more plausible parameter would be $L_{min} + KC$, where K is a constant combining 'dark noise' in the visual system (Barlow, 1957) and light scatter in the eye (Whittle, 1986). However, if the area over which luminance were pooled in setting the gain were not localized to L_{min} (which in the sine-wave condition is an infinitesimally narrow line), but was instead of finite width, that finite width would become an increasing proportion of the duty cycle of the stimulus as spatial frequency increased. Drift eye movements occurring during fixation could help to spread the region over which the luminance that sets the adaptational level was pooled. In the limit, if the spatial frequency were enough for the pool to be as large as a complete cycle of the stimulus the gain factor would become L_{mean}. Unfortunately we have no independent means of assessing the value that K might take, so we conclude that while optical attenuation probably accounts for most of the lack of a dip-down in ΔC at high C, adaptational pooling may be also be partly responsible. The appendix shows how both the effects of optical attenuation and adaptational pooling can be included in a general formulation for predicting the function describing ΔC as a function of C based on a power law for W model.

Number of discriminable steps in contrast

Having measured contrast discrimination thresholds throughout the range of pedestal contrasts we are in a position to answer the question: how many discriminable steps in contrast are there? For an increment, the upper physical limit for luminance is unspecifiable and, therefore, so is the number of discriminable steps in contrast. For decrements and periodic stimuli, however, the number of discriminable steps, or N, in contrast is finite and hence calculable. To estimate N we employed a function which described the data with a very high degree of accuracy:

$$\Delta C = k\,(C/(1+K))^n.\,(1 - C/(1+K))^{2-n} \qquad (1)$$

in which we allow k, n and K to be free parameters. This is similar in form to equation (A9) derived in the Appendix for including the effects of optical attenuation and adaptational pooling, but has one less free parameter. We stress that equation (1) is not meant to be a model of performance, but merely a convenient way of fitting the data with a curve which we can then use to obtain N. Using equation (1) we found N by a process of iteration between the value of C = contrast threshold and $C = 1$. The results, in Table 1, show that N varies significantly between conditions and subjects, but the principle source of variation appears, as one would expect, to be spatial frequency. The mean values of N averaged across the sine-wave and square-wave data, and across subjects is 55, 69, 47 and 35 for the 0.125, 0.5, 4.0 and 8.0 c/deg conditions, respectively. These values are consistent with an inverse U-shaped function of N with respect to spatial frequency under the conditions used in this study, though more data are clearly required to find the precise shape of the function. The estimates of N at 0.125 c/deg are lower than those at 0.5 c/deg principally because the values of k are larger in the 0.125 c/deg condition. k might provide an estimate of the amount of noise in the system and if so this may be consistent with there being a lower sampling density of detectors per unit cycle of the stimulus in the 0.125 c/deg condition compared to the 0.5 c/deg condition. On the other hand, the lower values of N at 4.0 and 8.0 c/deg reflects the increased value of K for these conditions. This is consistent with the role of either the optics and/or adaptational pooling described in the previous sections. Finally it is worth reiterating the fact that a simple power law in C fit to the data points for $C < 50\%$ contrast (see Table 1) predicts lower values of N than estimated here.

REFERENCES

Barlow, H. B. (1957). Increment thresholds at low intensities considered as signal noise discrimination. *Journal of Physiology, 136*, 469–488.

Blakemore, C. & Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology, London, 203*, 237–260.

Blakemore, C., Muncey, J. P. J. & Ridley, R. M. (1973). Stimulus specificity in the human visual system. *Vision Research, 13*, 1915–1931.

Bradley, A. & Ohzawa, I. (1986). A comparison of contrast detection and discrimination. *Vision Research, 26*, 991–997.

Bowen, R. W. & Wilson, H. R. (1994). A two-process analysis of pattern masking. *Vision Research, 34*, 645–657.

Burr, D. C., Ross, J. & Morrone, C. (1985). Local regulation of luminance gain. *Vision Research, 25*, 717–727.

Campbell, F. W. & Gubisch, R. W. (1966). Optical quality of the human eye. *Journal of Physiology, London, 186*, 558–578.

Campbell, F. W. & Kulikowski, J. J. (1966). Orientation selectivity of the human visual system. *Journal of Physiology, London, 187*, 437–445.

Crawford, B. H. (1947). Visual adaptation in relation to brief conditioning stimuli. *Proceedings of the Royal Society B, 134*, 283–302.

Foley, J. M. (1994). Human luminance pattern-vision mechanisms: Masking experiments require a new model. *Journal of the Optical Society of America A, 11*, 1710–1719.

Foley, J. M. & Legge, G. E. (1981). Contrast detection and near-threshold discrimination in human vision. *Vision Research, 21*, 1041–1053.

Georgeson, M. A. & Georgeson, J. M. (1987). Facilitation and masking of briefly presented gratings: Time course and contrast dependence. *Vision Research, 27*, 369–379.

Gottesman, J., Rubin, G. S. & Legge, G. E. (1981). A power law for perceived contrast in human vision. *Vision Research, 21*, 791–799.

Greenlee, M. W. & Heitger, F. (1988). The functional role of contrast adaptation. *Vision Research, 28*, 791–797.

Hayhoe, M. M., Benimoff, N. I. & Hood, D. C. (1987). The time course of multiplicative and subtractive adaptation processes. *Vision Research, 27*, 1981–1996.

Jamar, J. H. T. & Koenderink, J. J. (1984). Dependence of contrast detection and independence of AM and FM detection on retinal illuminance. *Vision Research, 24*, 625–629.

Kingdom, F. & Moulden, B. (1991). A model for contast discrimination with incremental and decremental test patches. *Vision Research, 31*, 851–858.

Kohayakawa, Y. (1972). Contrast-difference thresholds with sinusoidal gratings. *Journal of the Optical Society of America, 62*, 584–587.

Legge, G. E. (1981). A power law for contrast discrimination. *Vision Research, 21*, 457–467.

Legge, G. E. & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America, 70*, 1458–1471.

Legge, G. E. & Kersten, D. (1983) Light and dark bars; contrast discrimination. *Vision Research, 23*, 473–483.

Legge, G. E., Kersten, D. & Burgess, A. E. (1987). Contrast discrimination in noise. *Journal of the Optical Society in America A., 4*, 391–404.

Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *Journal of the Acoustical Society of America, 49*, 467–477.

MacLeod, D. I. A., Williams, D. R. & Makous, W. (1992). A visual nonlinearity fed by single cones. *Vision Research, 32*, 347–363.

Naka, K.-I. & Rushton, W. A. (1966). S-potentials from luminosity units in the retina of fish (Cyprinidae). *Journal of Physiology, 185*, 587–599.

Ross, J. & Speed, H. D. (1991). Contrast adaptation and contrast masking in human vision. *Proceedings of the Royal Society of London B, 246*, 61–69.

Shapley, R. & Enroth-Cugell, C. (1984). Visual adaptation and retinal gain controls. *Progress in Retinal Research, 3*, 263–346.

Swanson, W. H., Wilson, H. R. and Giese, S. C. (1984). Contrast matching data predicted from increment thresholds. *Vision Research, 28*, 457–459.

Whittle, P. (1986). Increments and decrements: Luminance discrimination. *Vision Research, 26*, 1677–1691.

Whittle, P. (1993). Brightness, discriminability and the "crispening effect". *Vision Research*, *32*, 1493–1507.

Wilson, H. R. (1980). A transducer function for threshold and suprathreshold human vision. *Biological Cybernetics*, *38*, 171–178.

APPENDIX

Whittle (1986) found that if contrast is measured as $W = (L_{max} - L_{min})/L_{min}$, rather than $C = (L_{max} - L_{min})/(L_{max} + L_{min})$ then the contrast discrimination function for both incremental and decremental test patches followed the rule

$$\Delta W = kW^n \tag{A1}$$

where n was found to be approximately unity. Following Fechner's integration of Weber's law, we assume that contrast discrimination reflects the operation of a transducer function, $R(W)$, in which a fixed value of $\Delta R(W)$ represents the criterion level of discrimination. Thus since $\Delta W/W^n$ is a constant

$$\Delta R(W) = \Delta W/W^n.$$

If ΔW is small this can be approximated in the limit by

$$dR(W) = 1/W^n \, dW. \tag{A2}$$

Integrating both sides of equation (A2) gives

$$R(W) = 1/(1-n)W^{(1-n)} \qquad n! = 1 \tag{A3}$$

or

$$R(W) = \ln W \qquad n = 1.$$

It is easily shown that $W = 2C/(1 - C)$ and therefore the transducer function $R(W)$ in equation (A3) can be reformulated in terms of C as

$$R(C) = 1/(1-n)\,[2C/(1-C)]^{(1-n)}. \tag{A4}$$

To formulate the expected relationship between ΔC and C, one simply performs the reverse of Fechner's integration by first taking the derivative of equation (A4) with respect to C. Thus

$$\frac{dR(C)}{dC} = 2^{1-n}C^{-n}(1-C)^{n-2} \tag{A5}$$

Taking the reciprocal of the result and adding back the constant k then gives

$$\Delta C = k\,2^{n-1}\,C^n\,(1-C)^{2-n} \qquad n! = 1 \tag{A6}$$

or

$$\Delta C = k\,C\,(1-C) \qquad n = 1. \tag{A7}$$

Equations (A6) and (A7), like their equivalent in terms of ΔW, equation (A1), implausibly predict ΔC to be zero when $C = 1$. Dark noise (Barlow, 1957), light scatter (Whittle, 1986) and adaptational pooling will prevent L_{min} reaching zero (and hence $C = 1$). If K reflects the combined effect of these three factors, we can replace L_{min} with $L_{min} + KC$ in the denominator of $R(C)$, which then equals $[1/(1-n)]\,2C/(1 - C + CK)$. Using the above method it is easily shown that with the addition of K

$$\Delta C = (k/2)\,(2C)^n\,(1 - C + KC)^{2-n}. \tag{A8}$$

Finally, if we wish to include the effects of optical attenuation by an amount a, where a = retinal contrast/physical contrast, equation (A8) now becomes

$$\Delta C = (k/2)\,(2aC)^n\,(1 - aC + aKC)^{2-n} \tag{A9}$$

or more simply

$$\Delta C = k'\,C^n\,(1 - aC + aKC)^{2-n}. \tag{A10}$$