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LOCAL REGULATION OF LUMINANCE GAIN

DAVID C. BURR, JOHN ROSS and M. CONCETTA MORRONE
Department of Psychology, University of Western Australia, Nedlands, WA 6009, Australia

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Abstract—Contrast sensitivity was measured for sinusoidal gratings sampled by compressing luminance into a variable number of sample bars. This procedure does not affect the amplitude or mean luminance of the grating, but does increase the local luminance of the sample bars: the fewer the bars, the more luminous they are. It was found that sensitivity increased with bars per cycle, particularly at low spatial frequencies. Further experiments, in which the local luminance of the sampling bars (but not the average luminance of the grating) was varied by addition of veiling glare showed that contrast sensitivity varied inversely with local bar luminance (a Weber type relationship). We interpret the results as evidence of local gain control under conditions where average luminance, and hence mean photon flux, does not vary. Calculations based on variation of sensitivity with spatial frequency suggest that gain control can be very localized, with receptive fields of Gaussian space constant of 0.5′ arc. The relevance of these results to modern psychophysical concepts, including the definition of contrast is discussed.

INTRODUCTION

Under a wide variety of conditions vision obeys Weber's law: the incremental threshold is proportional to the background luminance. Evidence to substantiate this statement traces back to Bouguer who, in 1776, used pairs of candles to establish a Weber constant of about 1/64 for luminance. However Weber's Law breaks down under some conditions: at low luminances, for small or briefly exposed spots of light (e.g. Barlow, 1957; but see also Cornsweet and Pilsner, 1965), and for gratings of high spatial or temporal frequency (Van Nes *et al.*, 1967). Under these conditions incremental thresholds increase not in proportion to background luminance, but to its square root, suggesting that the limit sensitivity is set by photon noise (DeVries, 1943; Rose, 1948) which increases with the square root of photon flux.

Weber's law implies a change in visual sensitivity, that is adaptation of the visual system to changing illumination. But, as Shapley and Enroth-Cugell (1984) point out in their extensive review of visual adaptation and retinal gain controls, Fechner (1860) deduced the wrong mechanism to explain Weber's law. He proposed a form of response compression: that visual response is a logarithmic function (a "very shallow saturating function") of stimulus intensity. What happens in fact is that gain, the ratio of output to input, is automatically adjusted downwards as stimulus intensity increases. The visual response curve is shifted rightwards as luminance increases. The whole of the stimulus range is not compressed onto the response range of visual units. Rather, a limited stimulus range is covered at each background level, its extent and the slope of the response function being determined by the prevailing gain.

It has sometimes been assumed that gain is not automatically adjusted under conditions where the square root law, rather than Weber's Law, applies (e.g. Barlow, 1964). But, as Shapley and Enroth-Cugell point out, the fact that sensitivity is photon limited does not imply that gain is not adjusted. It might or might not be. Weber's law implies adaptation. The square root law does not, because it can be explained on photon considerations: but it does not exclude adaptation, nor change in gain as the mechanism of adaptation. In this study we ask whether gain is changed automatically under conditions where the square root law applies.

A second issue addressed by this study is the regionality of gain control: to what extent is gain control localized? The fact that apparent brightness is determined principally by border contrast suggests that gain must be localized to some extent (Shapley and Tolhurst, 1973). However, at least for scotopic vision there is good evidence for spread of gain, or what Rushton (1965b) terms "adaptation pooling". Rushton (1965a) showed sensitivity variations with luminance at luminance levels so low that only a small fraction of rods receive photons. This implies that adaptation does not occur in the individual rods, but in "rod pools". The effect has also been confirmed in studies of cat ganglion cells (Enroth-Cugell and Shapley, 1973). Rushton conducted several other experiments aimed at proving the existence of rod adaptation pools (summarized in Rushton, 1965b), but some of these have failed on replication (e.g. Barlow and Andrews, 1967).

At photopic luminances, the results are less clear. Techniques like Rushton's which rely on photon paucity are inapplicable in ample light. While there is some evidence of spread of gain for the cone system (e.g. Yonemura, 1962; Westheimer, 1967) these results are far from conclusive.

For our experiments, we take advantage of the fact that there exist in the brain motion sensitive units with large receptive fields, at least up to 5° in extent, and probably larger (Burr and Ross, 1982). There is evidence that these units summate over the extent of their receptive fields (Burr, 1981; Burr and Ross, unpublished data), and that they are tuned for a particular spatial frequency (Anderson and Burr, 1985). We measure not increment thresholds for isolated spots of light, but contrast sensitivity for a sinusoidal grating, when it is sampled and displayed in a way which changes the local luminance of the samples carrying the information about that harmonic, but not the average luminance (and hence photon flux) of the stimulus. Varying the spatial frequency and sampling rate of the grating allows us to investigate the summation zone for gain control.

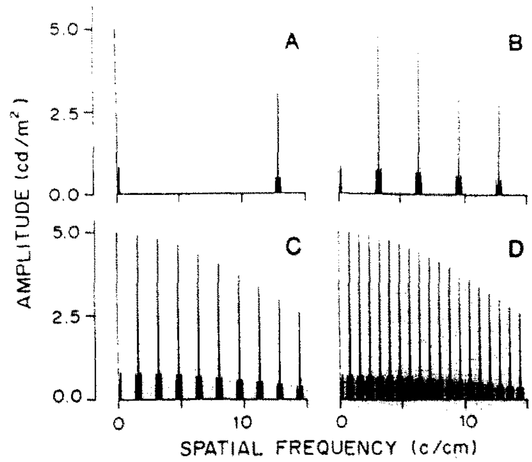

Fig. 2. The Fourier transforms of the profiles of Fig. 1. The mean luminance (0 cycles/cm) and the fundamental sinusoid (0.2 cycles/cm) are practically identical for the four conditions. What sampling does is to introduce a string of spurious high spatial frequencies at a repetition frequency determined by the sampling rate.

METHODS

Stimuli

Stimuli were presented on the face of a Hewlett Packard X-Y display (model 1317A) using a raster display technique. Both the X-(timebase) and Z-(intensity modulation) axes were driven by computer (Cromemco Z-2D), while the Y-(high speed raster) axis was generated by a 1 M Hz triangle wave of a triggered function generator (Krohn-Hite Model 5300A).

To the X-axis was sent a staircase waveform, 256 elements long and varying in step size from 1 to 16 elements. To the Z-axis was applied a sinusoidal waveform of 4 cycles (either in phase with the X-axis staircase, or with steadily increasing phase so as to cause the waveform to drift at 5 Hz). The effect of the staircase on the X-axis is to compress the sinusoidal waveform at sampling points, the frequency of which varies with staircase step size. A step size of 1 created 256 lines, or 64 samples for each of the 4 cycles, whereas a step size of 16 produced 16 lines, or 4 samples per cycle (twice the Nyquist rate). For all staircase step sizes, the average screen luminance remained the same, 5 cd/m^2 (verified by photometer measurements). The frame frequency was 320 Hz.

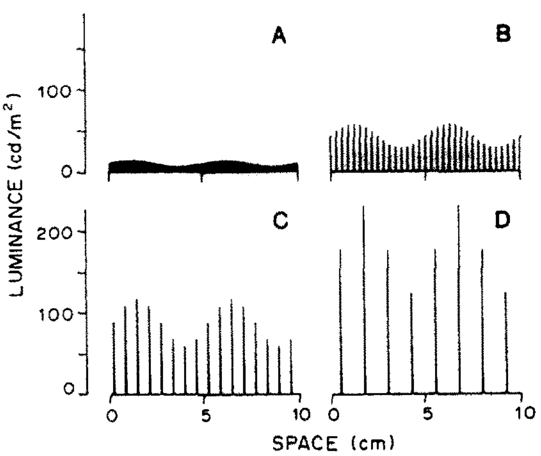

Fig. 1. The profiles of the four stimuli used in these experiments. All contain four cycles of grating in which the luminance has been compressed into narrow sample bars: (A) 64 samples/cycle, (B) 16 samples/cycle, (C) 8 samples/cycle, (D) 4 samples/cycle. As a result of the compressive sampling, both the local luminance and the local amplitude of modulation at the sampling points is higher for the course sampled than for the fine sampled gratings. However, as Fig. 2 shows, the average luminance and amplitude of the sampled sinewave is practically equal for all conditions.

Figure 1 describes the luminance profiles produced by the above procedure. These were obtained by measuring local luminance of the oscilloscope face with a Photometer (Spectra-Prichard Model 1980A-PL) while the stimuli (bars and sinewave together) were caused to drift slowly. The analogue output signal from the photometer was read by the Cromemco computer, which later plotted the luminance profile. Figure 2 shows the Fourier transforms (calculated digitally on a Digital PDP-11/60 computer). They show that for each sample rate the amplitude of the sinewave grating is virtually identical, but the coarse samples show additional high frequency harmonics.

Figure 3 is an attempt to reproduce photographically the stimuli. They are not entirely accurate, because of the compressive gamma of photographic film (a problem not encountered in our experiments, as we relied on temporal summation for intensity control), but they give an impression of the appearance of stimuli when they are stationary.

For the majority of measurements the sinusoidal gratings, but not their sample bars were caused to drift. This was achieved by steadily incrementing the phase of the sinusoidal waveform (which went to the Z-axis) while the staircase waveform to the X-axis remained constant. The effect on each individual bar was to cause it to modulate sinusoidally in intensity.

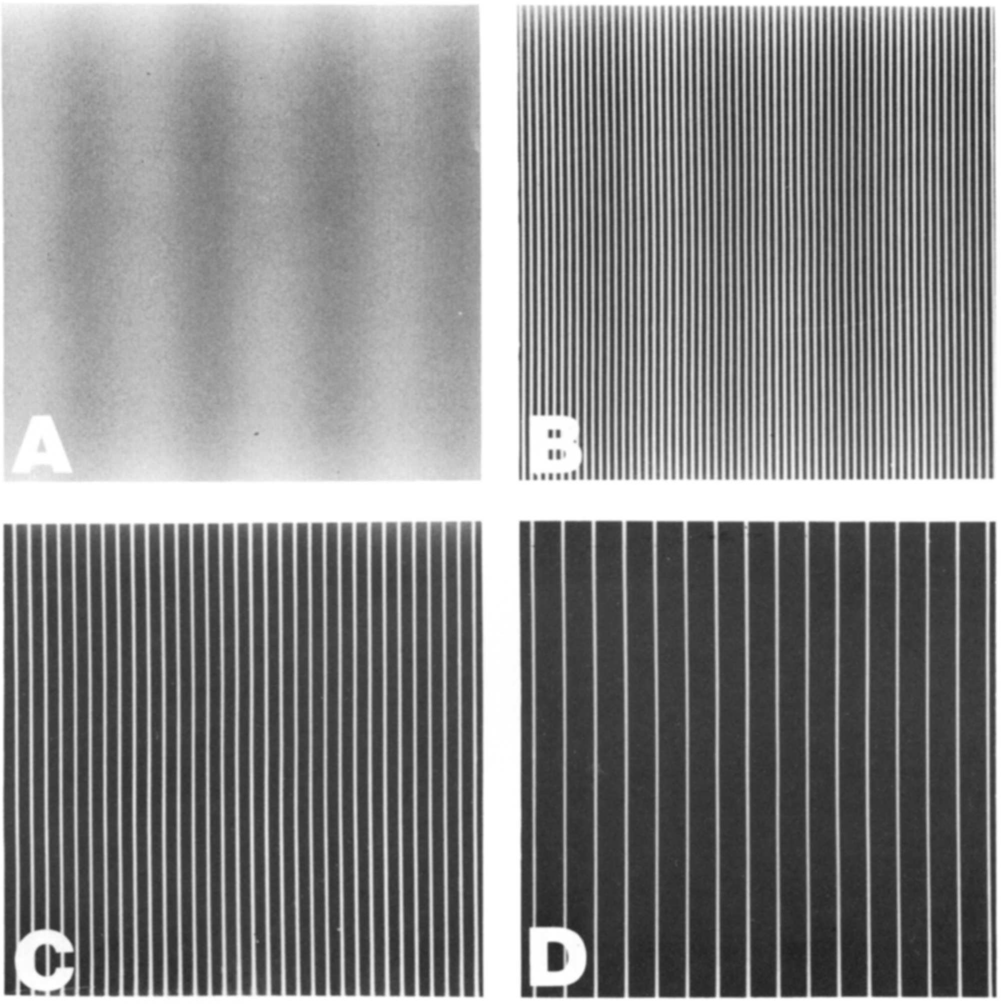

Fig. 3. Photographs of the stimuli used in these experiments. These are not exact reproductions, as no photographic film is linear over the required range, but they give an impression of the appearance of sampled gratings when stationary. On very close viewing (with a positive lens to aid accommodation if required) only in (A) is the grating visible. With increasing distance, the grating begins to emerge in the other photographs.

The overall effect was to create the appearance of a "phantom" grating drifting past stationary bars.

General techniques

Contrast thresholds were measured by the method of adjustment. Contrast was varied by the observer who adjusted a handheld potentiometer determining the voltage level of one of the computer's analogue inputs. The exponential of this level was then output to a D/A and multiplied analogically with the sinusoidal waveform. When the observer indicated satisfaction with his threshold setting, the computer recorded the threshold contrast and presented the next trial. In the case of drifting gratings, threshold was always set so that the direction of motion could just be discerned.

For all measurements, four cycles of grating were displayed on the screen, masked down to a circle of 20 cm diameter. Spatial frequency was varied, where appropriate, by varying viewing distance. A frequency range of 0.07–20 c/deg was achieved by varying viewing distance from 19 cm to 57 m, using two front silvered mirrors to help achieve the larger distances.

Veiling glare

One experiment required the superimposition of a veiling glare of uniform luminance on the stimuli. This was achieved with a second oscilloscope (Joyce Electronics) lit to a uniform luminance of 5 cd/m^2 (to match that of the Hewlett-Pachard). The oscilloscope faces were covered with mutually orthogonal sheets of polaroid film. They were optically superimposed by means of a half silvered mirror and viewed through a wheel of polaroid sheeting. Rotating the polaroid sheeting (with a stepping motor driven by the computer) varied the proportional contribution of each oscilloscope without significantly affecting the total luminance of the display, of 2.5 cd/m^2 (after attenuation by the half silvered mirror). Six proportions of stimuli to glare were used, varying from 15 to 100%. Before each session, the proportional luminance and effective contrast at each setting was automatically calibrated by photometer measurements of maximum and minimum luminances, with and without the veiling glare.

This method caused the mean local luminance of the sample bars to vary, while leaving the average luminance constant. For example, when the rotatable polaroid was set at 45°, the contribution from the glare was 1.25 cd/m^2 and that from the stimulus 1.25 cd/m^2, totalling 2.5 cd/m^2. However, the mean luminance of each bar was now reduced from 80 cd/m^2 (polaroid set at 90°) to 41.25 cd/m^2 (40 cd/m^2 from the stimulus plus 1.25 cd/m^2 from the glare).

RESULTS

The reader can gain for himself an impression of the effect of sampling on visibility for various spatial frequencies by observing the photographs of Fig. 3. All contain a sinusoidal grating of about 20% contrast, sampled at rates from 64 samples per cycle [Fig. 3(A)] to 4 samples per cycle [Fig. 3(D)]. On close viewing, the grating of Fig. 3(A) is far more visible than the others, although all the gratings have the same amplitude. With increasing viewing distance, the other gratings begin to emerge, until they are all equally visible.

Fig. 4 shows the results of the measurements of contrast sensitivity, for the four sampling conditions, both for stationary and for drifting gratings. The stationary thresholds were for seeing a grating, and the drifting thresholds for seeing movement. At low spatial and sample frequencies observers reported seing a "phantom grating" drifting between the stationary sample bars.

At low spatial frequencies, there is a clear advantage for the high sampling rate, particularly when the grating is drifting. The difference between sensitivity for the 4 and 64 sample/cycle grating is about 1.25 log units. This advantage is steadily reduced with increasing spatial frequency, until gratings are equally detectable at all four sampling frequencies. The fact that sensitivity is equal at large viewing distances demonstrates that the amplitude of the harmonic is equal in all cases.

The greatest effects were seen with drifting gratings. This is to be expected, as the higher sensitivity at low spatial frequencies when gratings are drifting provides a greater range for effects of sampling to show themselves. Indeed at very low spatial frequencies, a stationary grating was never seen at 4 samples/cycle, thus providing no range at all. All further measurements of effects at low spatial frequency were made with gratings drifting at 5 Hz. A frequency of 0.2 c/deg was chosen as a representative for study, as the curves for the four conditions are virtually parallel at this point.

High frequency masking?

A common explanation for the destructive effects of sampling on visibility has been that the spurious spatial frequencies introduced by sampling mask the lower frequencies which survive the sampling (Harmon and Julesz, 1973). We examined this possibility by measuring sensitivity for a sinusoidal grating in the presence of a high frequency mask equal in amplitude (but not in phase) to the spurious sampling frequencies. The mask was constructed by taking the Fourier transforms of the sampled gratings (Fig. 2) and scrambling the phase of the harmonics.

Figure 5 shows sensitivity measures as a function of sample rate for three conditions: the sampled gratings of Fig. 1; the same gratings with the phase of the spurious frequencies scrambled; the same gratings with the phase of the spurious frequencies scrambled and their orientation rotated through 90°.

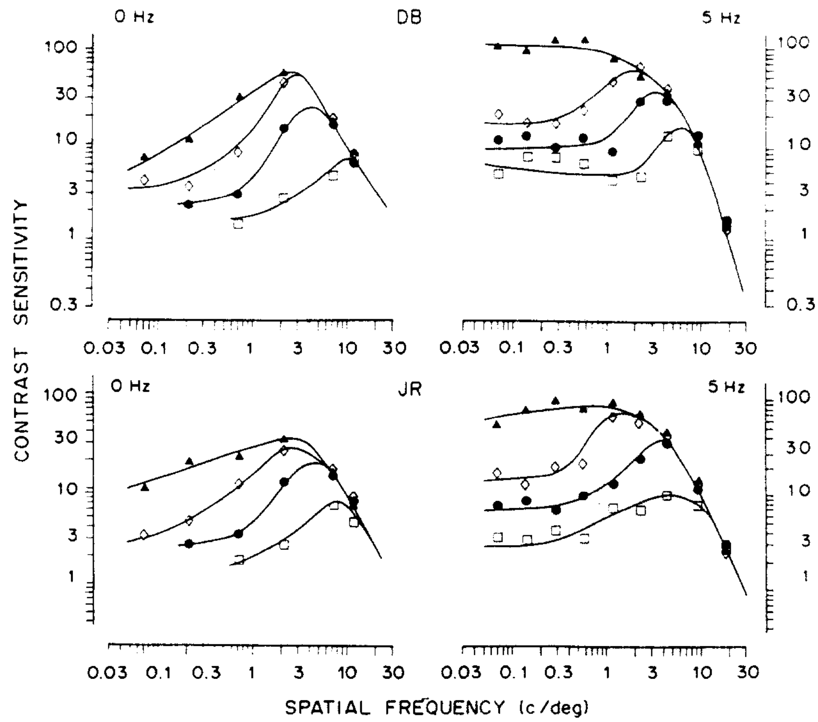

Fig. 4. Contrast sensitivity as a function of spatial frequency for stationary and drifting gratings, for the four sample conditions (solid triangles 64, open diamonds 16, solid circles 8, open squares 4 samples per cycle). At low spatial frequencies, the finely sampled grating was far more visible, while there is virtually no difference at 20 c/deg. At very low frequencies, the stationary grating was never visible at the lower sampling rates.

The greatest effect by far is found with the coarsely sampled gratings of intact phase. Here, sensitivity is about 1 LU greater for 64 samples/cycle than for 4 samples/cycle. After phase scrambling, this effect is reduced to about 0.3 LU. Clearly, the bulk of the effect can not be explained by "critical band masking" of the type proposed by Harmon and Julesz (1973).

Interestingly, the masking effect of the scrambled noise is no weaker after it has been rotated through 90°. This is strange, as masking effects tend to be orientationally selective (Campbell and Kulikowski, 1966; Anderson and Burr, 1985), and leads us to suspect that even the small impairment of sensitivity by the scrambled high frequencies is not a simple critical band masking effect.

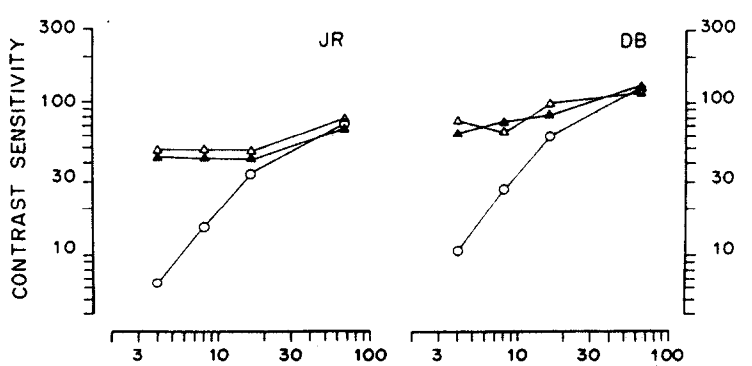

Fig. 5. Critical band masking. High frequency masks equivalent in spatial frequency and in amplitude to the spurious frequencies of the sampled conditions, but differing in phase were created by scrambling the phases of the harmonics in the Fourier transform of the sampled gratings. The solid triangles show sensitivity for seeing a grating in the presence of this mask, orientated parallel to the grating, and the open triangles sensitivity for when the mask was orientated orthogonally to the grating. The open circles are the thresholds for the sampled gratings, superimposed on a field of mean luminance to equilibrate the contrast of the spurious gratings with that of the masks. Neither of the phase scrambled masks reduced significantly sensitivity of the test grating.

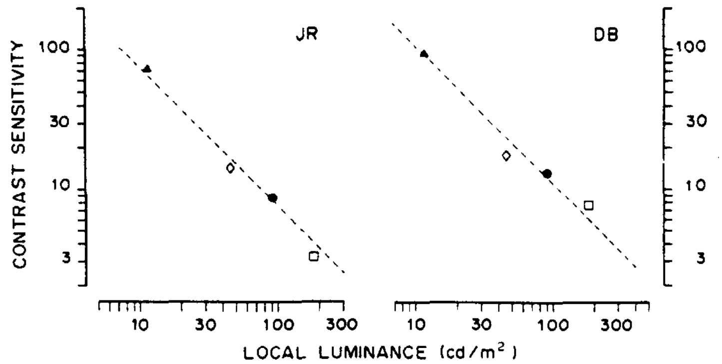

Fig. 6. Sensitivity for detection of a 0.2 c/deg grating drifting at 5 Hz (25 deg/sec), plotted against the average local luminance of the sample bars. The symbols represent the four sample conditions: 4 (open squares), 8 (solid circles), 16 (open diamonds) and 64 (solid triangles) samples/cycle. The dotted lines have slope of -1.

Local luminance

A more plausible explanation for the variation of sensitivity with sample rate emerges on considering Fig. 6. It shows contrast sensitivity measurements (taken from Fig. 4) plotted against the average local luminance of the sample bars, which varies inversely with sampling frequency. The results are well fitted by a straight line of slope -1. As the abscissa and ordinate are both logarithmic, this implies a hyperbolic relationship between contrast sensitive and local luminance: $\mathrm{CS} \propto 1/L_{\mathrm{loc}}$.

Veiling glare

The relationship between sensitivity and local bar luminance was examined more closely by means of veiling glare. Mixing the stimulus display with a veiling glare of the same mean luminance, we were able to vary the local luminance of the sample bars in finer steps than those shown in Fig. 6 (see Methods section). It also gave us another method of varying local but not average luminance without affecting the spatial distribution of the stimulus. Added glare does, however, vary the Fourier transform of the stimuli, by attenuating the spurious harmonics associated with the d.c. (the central, higher delta functions in the groups of three deltas shown in Fig. 2).

The results of sensitivity measures for the 4 sample rates, with 6 mixes of glare are presented in Fig. 7, as a function of local bar luminance. The straight lines are the regression lines of sensitivity against luminance, calculated from the raw data. These lines have slope of -1.0 for DB and -1.1 for JR, with correlation coefficients of -0.94 and -0.96. Again, the near unity slopes show that contrast sensitivity is inversely proportional to local luminance, whether

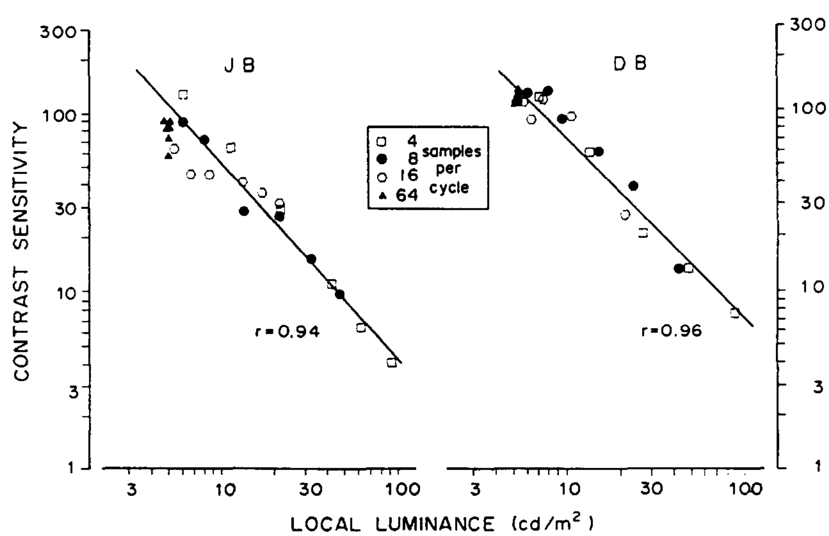

Fig. 7. Sensitivity for detection of a 0.2 c/deg grating drifting at 5 Hz (25 deg/sec), plotted against the average local luminance of the sample bars. Measurements were made for the four sample frequencies, each mixed with 6 levels of veiling glare. Each point is the average of five measurements. The regression lines were fitted by least squares fit to the unaveraged data.

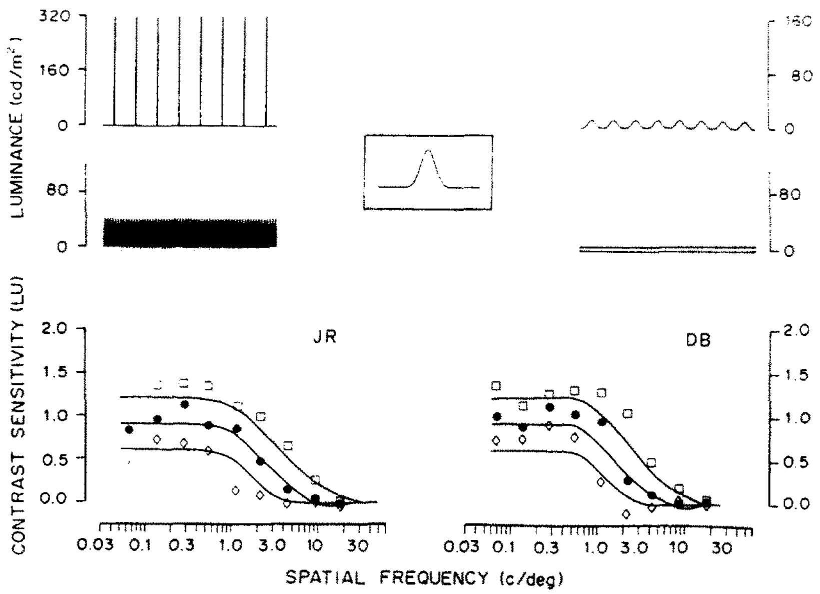

Fig. 8. *Above*. An example of how convolution with a Gaussian profile smooths the peaks of the sampled waveforms, yielding lower peak local luminance. *Below*. The data points represent the relative attenuation of the 4, 8 and 16 sample/cycle conditions, calculated from the right-hand curves of Fig. 4, by dividing the sensitivity for the 64 sample/cycle condition by that for the others. The curves are the theoretical attenuation in sensitivity, based on the local luminance after convolution with a Gaussian profile of 0.42′ for JR and 0.6′ for DB.

the local luminance be varied by sample rate or by addition of veiling glare.

The fact that a line of unit slope fits all these data, irrespective of whether luminance was varied by sampling rate or by veiling glare, is further evidence that masking by spurious harmonics is unlikely to be the sole explanation of the results: the composition and amplitude of the harmonics is quite different for the two methods of altering local luminance.

Adaptation pools?

Figure 4 shows that as the size of the stimulus is reduced (increasing its spatial frequency) the impairment of sensitivity by coarse sampling becomes progressively less. So far we have assumed that the local luminance of the oscilloscope determines exactly the local retinal luminance. This may be fair approximation for low spatial frequencies (where the curves are parallel) but it is not at high spatial frequencies. Firstly, the retinal image will be blurred by the optical system of the eye (Campbell and Gubish, 1966). Secondly, involuntary eye tremor will also smear the image (Carpenter, 1977). Thirdly, the gain setting mechanism must have a finite summation region over which luminance is averaged. In this section we report an attempt to measure the size of this region, bearing in mind that the result will reflect summation due to optics and eye tremor, as well as neural summation.

We assume the summation region to be Gaussian. We take the luminance profile at the oscilloscope of the 4 stimulus types (from Fig. 1), scale them to correspond to the retinal spatial frequencies measured in Fig. 4, and then convolve these profiles with a Gaussian profile of variable width. An example of the effect of convolution is shown in the upper section of Fig. 8. There two waveforms of zero contrast, one of 8 samples/cycle and one of 64 samples/cycle, are convolved with a Gaussian of space constant of 0.5′ arc. The 8 cycle/sample grating previously made up of luminance spikes is now heavily smoothed, attenuating the sharp peaks of local luminance.

The process was repeated for all the conditions measured in Fig. 4. The peak local luminance was then measured, and its predicted effect on contrast sensitivity calculated, based on the relationship (established in Fig. 7) that $CS \propto 1/L$. As the predicted effect of local luminance on sensitivity is relative to the absolute sensitivity at a particular spatial frequency, it was calculated as relative attenuation (relative to the 64 sample/cycle condition), not as absolute sensitivity. The predicted attenuation for the 4,8 and 16 sample/cycle conditions equalled the peak luminance for those conditions (after convolution) divided by the peak luminance for the 64 sample/cycle condition. The values obtained by this procedure were interpolated to produce smooth curves, such as those shown in Fig. 8.

Figure 8 also depicts the experimentally measured attenuation for each sample condition and spatial frequency. These points were calculated from the values shown in Fig. 3, by dividing the contrast sensitivity for the 64 sample/cycle condition by that for the other sample rates.

The convolution was repeated for many Gaussian widths, and the predicted attenuation calculated, until a reasonable fit was obtained for experimental data points. The Gaussians which gave the best fit (those shown in Fig. 8) has space constants sigma of 0.6′ and 0.42′ for DB and JR respectively. As Fig. 8 shows, these curves fit the data reasonably well. Other summation profiles, such as rectangular were not examined, although these may also yield reasonable, or even better, fits.

These results are interpreted to reflect the size of the spatial summation region for gain. However, as three factors can contribute to this region—optics, eye tremor and neural summation—it must therefore be taken as an upper estimate of the neural summation pool. Interestingly, the summation observed here (Gaussian sigma of about 0.5′ arc) is of the same order that Campbell and Gubish (1966) find for optical blur with a 2 mm pupil. Thus it is possible that the entire summation observed here resulted from optical aberration, and that the summation pool is in fact even smaller.

DISCUSSION

We find that the threshold amplitude of a grating displayed by compressive sampling is proportional to the mean luminance of the sample bars carrying information. Thus there is a Weber like relationship between local bar luminance and global grating amplitude to threshold, but not between luminance and modulation amplitude of sampling bars.

There is already evidence (Burr, 1981; Robson and Graham, 1981; Burr and Ross, 1982; Anderson and Burr, 1985; and unpublished results from our laboratory) that detection thresholds for drifting gratings are determined not by local luminance fluctuations, but by the combined activity of all luminance fluctuations within about one cycle of grating. Our results confirm summation. With compressive sampling, both the local luminance (L) and the local amplitude (a) of modulation increase in such a way that the ratio of a/L at any one sample point is constant for all sample rates (see Fig. 1). If detection of the luminance fluctuation at a particular point followed Weber's law, and there were no summation of energy in neighbouring bars, sampling should not affect detection. Were detection to follow the Rose–De Vries law without summation, detection for bright bars of the coarse quantized gratings should be better than that for the dimmer bars of fine quantized gratings. Our results show clearly that this is not the case.

The possibility that the results are due to critical band masking by the spurious frequencies introduced by sampling can be discounted. A high frequency mask equal in amplitude to the spurious sampling frequencies proved relatively ineffective in reducing the detectability of an unsampled grating. The small effect that was observed was aspecific for orientation, which is atypical for critical band masking. Further evidence is that in the experiment of Fig. 7, local luminance was varied in two ways: by varying sampling frequency, and by addition of a veiling glare to the sampled gratings. These two methods affect differently the amplitude and spread of spurious high spatial frequencies, yet data points from all levels of veiling glare fell on the curve of unit slope.

It may also be objected that the observer in our experiments was not adequately adapted to the local luminance level. This is certainly true, as all our trials were randomly interleaved, but should not affect greatly the results. Light adaptation is rapid (Crawford, 1937), so observers were almost certainly adapted to the brighter stimuli by the time they made their threshold settings. In the case of the dimmer stimuli, this would not have been true, and small strips of retina, corresponding to where the bright bars of the previous coarsely sampled stimulus had appeared, may not have been fully dark adapted. However, as the range of luminances measured was not great (about 1.25 lm), this should have little effect on sensitivity (Craik, 1938), particularly as only small strips of retina were at risk. But to be certain, we measured thresholds at the low luminance condition (64 samples/cycle) with and without previous adaptation to the 4 sample/cycle condition and found no measureable effect.

Gain and photon fluctuation

Variation of sensitivity with luminance for full gratings of 0.2 c/deg drifting at 5 Hz follows the square root law over the luminance range used in this study (Burr, 1979). As mentioned earlier, while this evidence supports the notion that detection is noise limited under these conditions, it says nothing about the presence or absence of gain control mechanisms, provided that gain is regulated at a site subsequent to that at which the noise source sets the limit. The average luminance, and hence the mean photon count was constant throughout our experiments, despite variations in local luminance. Thus the observed changes in sensitivity with variation in sampling rate could not have resulted from photon fluctuation. We find, nonetheless, that the threshold contrast of the sampled grating as a whole (not luminance fluctuation of single bars) increases in proportion to the mean luminance of the sample bars. This Weber like relationship strongly implies regulation of sensitivity to a global pattern, the sampled grating, by a gain which is set by the local luminance of the sample bars.

Local gain control

The most economical explanation for the effect of sampling on detectability is that a local gain regulation occurs before summation and before detection. If this explanation is correct, summation pools for gain control can be small, of Gaussian space constant 0.5′ or less. This is in the same order as the optical line spread function, which predicts visual acuity reasonably well (Campbell and Gubish, 1966). Thus it appears that the mechanisms of gain control can have similar resolution to those which limit acuity.

These results may seem to be at odds with previous experiments (e.g. Rushton, 1965b) pointing to the existence of large adaptation pools, particularly for rod vision. However, it is not inconceivable that there exist in vision adaptation pools of various sizes, just as there exist cells with a range of receptive field sizes. Shapley and Enroth-Cugell (1984) have suggested that adaptation pools should be roughly the same size as the retinal neurons which they adapt, a claim backed by electrophysiological evidence (Enroth-Cugell and Shapley, 1973). In the present study it is reasonable to assume that cells with small receptive field size respond to the fine lines of Fig. 1(B–D), and it seems plausible to assume that these cells are regulated by adaptation pools of about the same size. Rushton's (1965a) experiments were carried out at low scotopic luminances, where one would expect that only cells with large receptive fields would be stimulated (e.g. Van Nes and Bouman, 1967; Ross and Campbell, 1978), and these should have correspondingly large adaptation pools.

The precise site of luminance gain control in man is not known, but evidence from animal recordings suggest that adaptation can occur at all retinal levels from photoreceptors to ganglion cells (see Shapley and Enroth-Cugell, 1984). The limited data available on monkey photoreceptors suggests that while cones adapt (Valeton and Norren, 1983; Baylor, personal communication), rods do not (Nunn and Baylor, 1982). If this is true for human photoreceptors, it would be consistent with adaptation pools at scotopic but not at photopic luminances.

Implications

The brightness of reflecting objects depends less upon their luminance than on the contrast between them and their background. Mach (1865) first suggested that there exists some process governing the sensation of brightness whose intensity depends on the ratio between object and background luminance. As Shapley and Enroth-Cugell (1984) argue, gain control can provide what Mach required, a mechanism to guarantee that visual response to reflecting objects remains relatively constant in changing conditions. But if gain is set by such local highlights as our results suggest, the concept of contrast itself requires reexamination.

Definitions of contrast depend on the stimulus being measured. 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. This has been termed the Weber contrast. For periodic waveforms, Michelson contrast (a/L) is normally used, where a is the amplitude of modulation, and L is the mean luminance. For irregular waveforms such as noise, contrast is RMS/L. All definitions include a normalization factor for luminance level, which is either the mean or background luminance level.

However, if gain control is as local as the present experiments suggest, mean or background luminance is not the most appropriate normalization factor. For example, for the waveforms used in this experiment, contrast sensitivity, defined in the usual way as amplitude divided by mean luminance, is not constant for different sampling rates, all of which are above the Nyquist sampling frequency. If contrast sensitivity were redefined as the amplitude of the sampled waveform divided by the local luminance of the bars carrying the information, contrast sensitivity would be constant for all sampling conditions (by inspection of Fig. 7). The same argument applies to small bright objects, such as a point or a line. Our results suggest that a more appropriate definition to the standard $(L_o - L_b)/L_b$ 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. This has the added advantage that contrast can never be greater than 1, bringing this definition into line with the Michelson definition, commonly used in modern psychophysics.

The regionality of gain raises questions about the application of current ideas about the linearity of the visual system. Although formal claims about linearity have been made only for one-dimensional stimuli at threshold (Campbell and Robson, 1968), many investigators, particularly those involved in image processing, would like to generalize the notion much further. Our results do not contradict evidence for linearity of individual units. Changes in sensitivity with luminance probably result from gain changes of linear neurons rather than a compressive nonlinearity of the neurons themselves (see Shapley and Enroth-Cugell, 1984). However, the combined action of many neighbouring linear units operating at different gain levels results in a global nonlinearity. This precludes the possibility of any global linear analysis which does not take into account local gain mechanisms.

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