

Quantal Noise and Decision Rules in Dynamic Models of Light Adaptation

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To evaluate some of the consequences of including probabilistic processes (e.g. quantal noise) in a computable model of light-adaptation dynamics, we considered the behavior of a general class of models. These models contain four stages: (1) early noise; (2) a deterministic filtering and gain-changing stage; (3) late noise; (4) a decision rule that is either an ideal (signal-known-exactly) detector or a peak-trough detector. With the ideal detector and without late noise, the observer's sensitivity as a function of mean luminance and temporal frequency is not affected by the filtering and gain-changing stage. Consequently, if the early noise is entirely quantal fluctuations, sensitivity will always be a square-root function of mean luminance and a uniform (flat) function of temporal frequency. This latter prediction is contradicted by all known data; either the ideal-detector is the wrong decision rule or sensitivity is almost always limited by sources of noise other than quantal fluctuations. With the peak-trough detector, however, with or without late noise, the observer's sensitivity as a function of temporal frequency does reflect the sensitivity of the low-level filtering and gain-changing stage. Late noise is needed, however, if the observer's sensitivity as a function of mean luminance is to go through both a square-root and a Weber region. Comparing these conclusions to similar work on the spatial frequency dimension highlights differences between the spatial and temporal frequency domains. Finally, on the basis of these analyses and evidence from the literature, we question whether quantal fluctuations limit visual sensitivity under any condition.

Noise Quantal fluctuations Ideal observer Light adaptation Dynamics Temporal frequency
Spatial frequency

INTRODUCTION

In constructing models to account for the results of psychophysical experiments, the question of whether to include probabilistic processes arises. Probabilistic processes can often be ignored with little loss in predictive power. Sometimes, however, they must be explicitly included if predictions are to be even approximately correct. The intrinsically probabilistic nature of light (variously called photon noise, quantal fluctuations, quantal noise) has often been suggested as a critical component for a model of light adaptation. The standard deviation of quantal fluctuations grows as the square-root of the light intensity. Psychophysical sensitivity has been reported to decrease approximately in proportion to the square-root of the adapting light intensity over a limited range of light intensities (e.g. Hess & Nordby, 1986; Kelly, 1972; van Nes, Koenderink, Nas & Bouman, 1967). Thus quantal fluctuations have frequently been invoked as an explanation under

these conditions (e.g. Barlow, 1956, 1957; DeVries, 1942; Rose, 1942, 1948; see reviews in Hood & Finkelstein, 1986). Consequently, as part of a broader effort to construct a computable and practical model of the dynamics of light adaptation (Graham & Hood, 1989), we decided to investigate the properties of a rather general class of models with and without probabilistic processes. This brief report describes several observations made in the course of comparing the predictions of such models to the psychophysical thresholds for flickering stimuli that varied in temporal frequency and mean luminance (e.g. the classic data of DeLange, 1952, 1954, 1958; see reviews of such data in Watson, 1986; Graham, 1989; Shapley & Enroth-Cugell, 1984). Some observations reported here are not new, but together they impose substantial and insufficiently-recognized constraints on the classes of models that are viable and useful descriptions of the visual processing of temporal stimuli. Comparing these observations to similar work on the spatial frequency dimension (particularly that of Geisler *et al.*, reviewed in Geisler, 1989) underscored the differences between the spatial frequency and temporal frequency dimensions.

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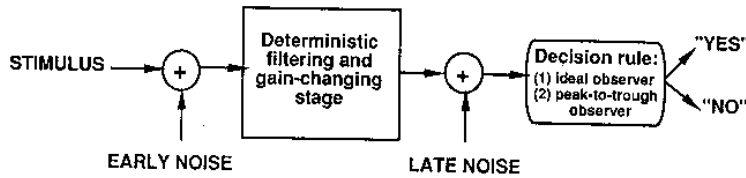


FIGURE 1. Diagram of class of models discussed here.

THE MODELS

A number of the models explicitly or implicitly assumed by others can be schematically represented as in Fig. 1 which shows the class of models we consider here. Models in this class can predict the response to any temporally-varying stimulus when other visual characteristics (e.g. spatial and wavelength content) are held constant. Each model in this class has four stages. The first is an early source of noise (which is where quantal noise can be included). The second is a deterministic temporal filtering and gain-changing stage; this stage has sometimes been identified with the receptors or the retinal ganglion cells. The third stage is another source of noise; the role of this late noise will be discussed briefly later. We will discuss here only the case where both the early and later noises are uncorrelated across time (as are quantal fluctuations). The fourth stage is a decision-rule. This last stage takes the response of the system, which is a function of time, and turns it into a psychophysical response from the observer—yes or no. A potentially infinite number of candidates for the decision-rule stage exist. We will look primarily at two of the most popular ones—the ideal observer and the peak-to-trough observer—which are described further below.*

*If one were to consider further decision rules, an attractive class would be those rules that pool responses at different points in time according to the following formula:

$$\int |r(t)|^k dt$$

where $r(t)$ is the response at time t (as suggested by Quick, 1974, and used by many since then; see review in Graham, 1989).

With an exponent in the range of about 3–5, the above rule is often used to model "probability summation". Briefly, let $r(t)$ be the average over many trials of a response that varies from trial to trial (and assume that the variability at different moments of time is independent). Let the above rule act on the average response $r(t)$ with an exponent (usually between 3 and 5) dictated by the slope of the psychometric function. Then this application of the above rule is a good approximation to what happens if the peak or peak-to-trough observer acts directly on each trial's noisy response. A peak-to-trough observer acting on a noisy waveform is computed here using Monte Carlo methods (e.g. middle panel, Fig. 3). Although the noise characteristics are somewhat different in the two cases, the predictions are probably quite similar.

With an exponent $k = \infty$, the above rule is equivalent to a peak detector acting on $r(t)$, which, for sinusoidally flickering stimuli, is equivalent to the peak-to-trough detector we have considered.

Notice there is only a single temporal filter in the class of models in Fig. 1 rather than multiple filters sensitive to different ranges of temporal frequency acting in parallel. To make the analogous assumption about spatial frequency would be foolish. The available evidence, however, suggests there is much less temporal frequency selectivity than there is spatial frequency selectivity. Thus starting for simplicity with a single temporal filter does not seem too misleading. (For a review of the evidence to this point see, e.g. Graham, 1989.)

Decision rules

In this paper we consider amplitude thresholds for sinusoidal flicker. The amplitude threshold is the minimal amplitude (the minimal difference between peak and trough luminances) at which an observer can just discriminate between a sinusoidally-flickering stimulus and

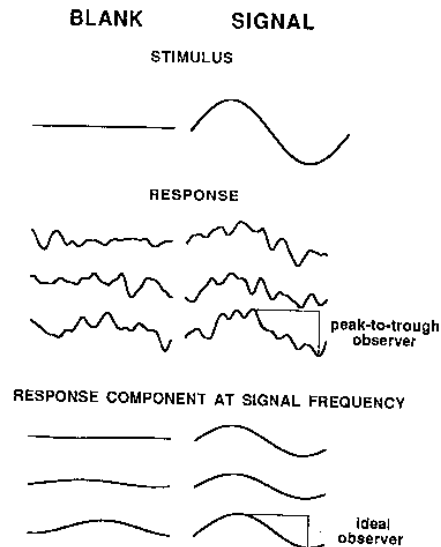


FIGURE 2. Luminance as a function of time is shown in the top row for a blank stimulus (left column) and a sinusoidal stimulus (right column). Typical responses of the models as a function of time are shown in the middle panel. The components of those responses at the signal frequency are shown in the bottom panel.

a blank stimulus. The luminance profiles for such stimuli are shown on the top right and top left of Fig. 2, respectively. The middle of Fig. 2 shows three examples of reponses from the model at the input to the decision

rule stage. Due to early and/or late noise, these responses are irregular functions of time.

The peak-trough observer rule is illustrated for the lower right response in the middle panel. It simply takes the maximum of each response and subtracts from it the minimum of each response. As is clear in the examples of Fig. 2, the particular moment in time where the peak or trough occurs varies from trial to trial, as does the peak-trough difference.

The ideal observer is the observer who performs as well as possible in the face of the noise in the system. We are going to consider the case *where the observer knows the frequency of the stimulus* on a given trial. (The case where the observer knows both the frequency and the phase of the stimulus is similar.) For sinusoidal flicker and noise that is uncorrelated across time, this ideal observer is essentially equivalent to an observer that first Fourier analyzes the response and then looks *only* at the Fourier component at the signal frequency.* The ideal observer ignores all the components at other frequencies. Such components are just as likely to have come from the blank stimulus as from the flickering stimulus and thus have no diagnostic power. The lower panel of Fig. 2 shows the components at the signal frequency for the six examples of response waveforms in the middle panel. Because these are noisy responses, the amplitude of the component at the signal frequency varies from trial to trial just as did the peak-trough difference.

To reiterate, there is an important difference between the behavior of the (frequency-known-exactly) ideal observer and the peak-trough observer. For the ideal observer, the only noise that matters is the noise at the signal frequency. But, as you can see in these middle waveforms, the peak-trough detector is potentially confused by noise at all temporal frequencies because the peak-to-trough difference is dependent on the response components at all temporal frequencies.

QUANTAL NOISE PREDICTIONS

This difference between the two decision-rules has a profound effect on their predictions for sinusoidally flickering stimuli as illustrated in the results of Monte Carlo simulations shown in Fig. 3. For these simulations, thresholds were computed for various temporal frequencies and mean luminances of sinusoidally flickering stimuli. The duration of the flicker (measured in seconds, not in cycles) was the same for all stimuli. The early noise stage was entirely quantal fluctuations and thus was independent of the stimulus frequency but increased with the square-root of the mean luminance. The deterministic stage consisted of four stages of feedback filtering of the kind used, for example, in Sperling and Sondhi (1968) and Martin (1968). And there was no late noise. Predictions were computed using both the peak-trough decision rule and the frequency-known ideal observer decision-rules (more precisely, using the amplitude of the Fourier component at the signal frequency, which is an extremely good approximation to the ideal observer in this situation).†

*In fact, the ideal observer for anything less than an infinite number of cycles departs slightly from this description. See, e.g. Geisler (1989) for more details. However, for the purposes of the present argument, this departure is insignificant. If phase as well as frequency were known, the ideal observer would examine only the component at the correct frequency and phase.

†For each frequency and mean luminance, 20 trials were run of a blank stimulus and 20 of the flickering stimulus at a given contrast. The value of d' was computed. (For the deterministic model, 1 trial was run at the given contrast and the value of the peak-trough computed.) Ideally, we should have used a number of different contrasts to find that value yielding the criterion value of d' (or peak-trough difference) at each temporal frequency and mean luminance. In fact, however, to do so would have required a good deal of time and seemed unwarranted since these calculations were done only to confirm the logical argument illustrated in Fig. 4. Instead, therefore, we let the amplitude of the flicker vary as the square-root of the mean luminance. (If predicted sensitivity were described exactly by a square-root law, this manipulation would have led to the same d' at all mean luminances. But predicted sensitivity is not described exactly by a square-root law.) And we then extrapolated to find the contrast producing a criterion d' . Before trying to quantitatively compare predictions of models like these to psychophysical thresholds, one would wish to avoid this extrapolation and actually do the predictions at different contrasts.

The calculations were programmed using MATLAB (from Math Works Inc.—on a Macintosh IIfx). The feedback model was calculated incrementally across time using difference-equation approximations to differential equations. (The differential equations can be found, e.g. in Sperling & Sondhi, 1968.) The equation for each stage of feedback was:

$$f_j(i) = f_j(i-1) + (\Delta t/\tau) \times \{f_{j-1}(i-1) - f_j(i-1) \cdot [1 + g \cdot f_n(i-1)]\}$$

where i indexes the discrete time steps. Δt is the length of each discrete time step, n is the total number of feedback stages, $f_j(i)$ (for $j = 1-n$) is the response of the j th feedback stage at the i th time step, $f_0(i)$ is the stimulus at the i th time step, τ is the time constant of each feedback stage, and g is the strength of the feedback from the last stage's output to each preceding stage.

We used four stages of feedback in the model ($n = 4$) where the time-constant of each stage (τ) was 45 msec. The model's response was calculated every 0.5 msec ($\Delta t = 0.5 \text{ msec}$) for a period of 1 sec of a flickering stimulus. There were always an integral number of cycles of flicker in this 1 sec period. The model's response to the flickering grating had settled down before this 1 sec period (which avoids transient effects due to the onset or offset of either the mean luminance or the flicker). We checked that the time interval and number of samples was great enough that the model's behavior was stable at the mean luminances and frequencies reported. The units of luminance used in the calculations were such that 1 unit corresponds to 10 td. In these units, the strength of the feedback g was set equal to 10. The vertical position of the curves in each panel (the absolute level of amplitude sensitivity for each panel) was essentially set arbitrarily by changing a multiplicative constant to make the curves occupy a range corresponding to typical psychophysical data. (Choosing this multiplicative constant corresponds to manipulating the fixed duration of the stimulus and/or the overall gain of the filters and/or the threshold criterion depending on which panel is under consideration.)

On each trial new samples of independent Gaussian noise were added at each point in time. Quantal fluctuations are actually Poisson rather than Gaussian but the Gaussian is a satisfactory approximation in the situation here.

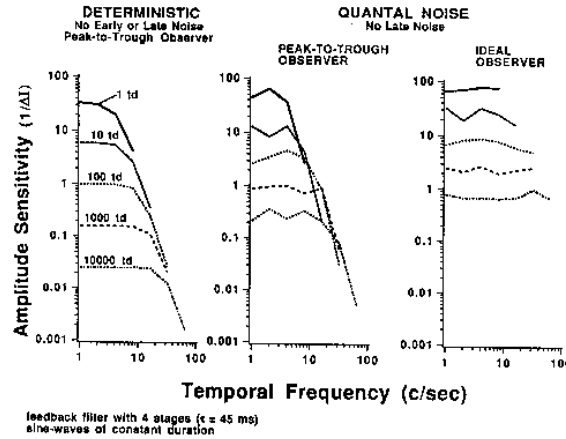


FIGURE 3. Predictions of three versions of the model as a function of the temporal frequency and mean luminance of flickering stimuli. The predictions of the deterministic stage in the absence of early or later noise is shown in the left panel. The predictions of the peak-to-trough observer and the ideal observer in the presence of quantal early noise are shown in the middle and right panels respectively.

For comparison, predictions were also computed from a stripped-down model consisting only of the deterministic stage and the peak-to-trough observer.*

Predictions as a function of temporal frequency

For all panels of Fig. 3, amplitude sensitivity (the reciprocal of the amplitude at threshold) is plotted logarithmically on the vertical axis, and temporal frequency is plotted logarithmically on the horizontal axis. Different curves come from different mean luminances. The left panel of Fig. 3 shows the predictions of the stripped-down deterministic model. These predictions resemble the psychophysical results. (This resemblance is no accident since it is why this kind of deterministic stage has been of interest in the past.) The predictions for the two decision rules differ dramatically from one another when quantal noise is included. For the peak-to-trough observer in the middle panel, the predictions are rather like those of the deterministic stage although they differ in ways mentioned below. For the ideal observer in the right panel, however, the predicted curves are entirely flat. That is, in spite of the fact that the deterministic stage dramatically attenuates higher frequencies as shown in the left panel, the ideal observer is equally sensitive to all temporal frequencies. How can that be?

Figure 4 attempts to provide the necessary insight. Here amplitudes are plotted logarithmically on the vertical axis and temporal frequency is plotted logarithmically on the horizontal. In the top row of graphs, the dotted lines represent all potential sine-waves of a particular amplitude, with the 2 and 16 c/sec signals

illustrated as solid points in the left and right panels respectively. The solid horizontal lines represent the noise. Since the noise is assumed to be quantal noise

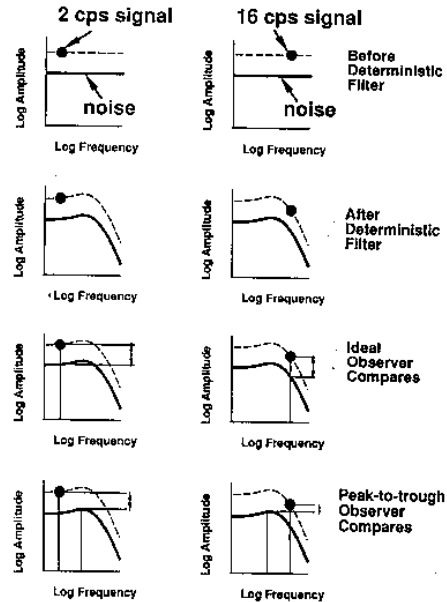


FIGURE 4. The top row shows the amplitude as a function of frequency for stimuli—the solid lines showing that for noise and the dotted lines for potential flickering stimuli all of the same amplitude. The solid points represent a 2 c/sec stimulus (left column) and a 16 c/sec stimulus (right column). The second, third, and fourth rows show the amplitude functions for the noise and stimuli after they have passed through the deterministic filtering stage. The third and fourth rows then illustrate the action of an ideal observer and a peak-to-trough observer, respectively, for discrimination of a 2 c/sec (left column) or 16 c/sec (right column) signal from a blank.

*Since there is no noise in this stripped down model, the true ideal observer also responds perfectly. An observer that calculates the amplitude of the Fourier component at the signal frequency leads to predictions exactly like those of the peak-to-trough observer.

(and the sinusoidal flicker is of the same duration for all frequencies), the noise has the same amplitude for all frequencies.

The graphs in the second row show the outputs after the deterministic-filter stage of the model. Both the signals and noise have gone through the same filter and thus have been multiplied by the same factor at a given frequency. Hence, the dashed line showing the amplitudes of filtered signals is simply a vertical translation on this log axis of the solid line representing the filtered quantal noise spectrum.

In the third row, the ideal observer, which is only concerned with noise at the signal frequency, compares the signal at 2 c/sec with the noise at 2 c/sec and compares the signal at 16 c/sec with the noise at 16 c/sec. Notice that the log distance between signal and noise is the same at 2 c/sec as it is at 16 c/sec. That is, the signal/noise ratios are equal for these two frequencies (and, more generally, all frequencies); hence these signals are equally detectable for the ideal observer.

The fourth row illustrates the situation for the peak-trough observer. Remember that this observer can be affected by the noise at all frequencies. This noise will tend to be dominated by the least attenuated noise—the noise at the peak of the function. (The fact that noise at all other frequencies also matters to some extent is ignored in Fig. 4.) So the peak-trough observer is comparing signals of all frequencies to much the same noise. Since the filtered 2 c/sec signal is bigger than the filtered 16 c/sec signal, the signal/noise ratio will be greater for 2 than for 16 c/sec, and so will the observer's sensitivity. In fact, since the peak-trough observer compares all filtered signals to much the same noise, the peak-trough observer's predicted sensitivities might be expected to closely reflect the filtered signal amplitudes. We saw in Fig. 3 that this was, in fact, true. In particular, the shapes of the curves in the left and middle panels are rather similar.

To summarize the points above: when there is no late noise, the ideal observer's predicted sensitivity does not depend on the deterministic stage at all; it is determined entirely by the early noise spectrum. For the case shown in Fig. 3—where the early noise is entirely quantal noise and the signals are sine-waves of constant duration—the early noise spectrum is flat and, therefore, so is the predicted sensitivity. This prediction is contradicted by large amounts of psychophysical data and makes the ideal observer in conjunction with quantal noise very unattractive as a component of computable model of the dynamics of light adaptation.

On the other hand, the predictions for the peak-trough observer (in the middle panel Fig. 3) do reflect the deterministic stage and hence can plausibly model psychophysical sensitivity even if quantal fluctuations are the only noise source.

However, as is described below, the peak-trough observer's predictions have a major problem when considered as a function of mean luminance.

Predictions as a function of mean luminance

Both the ideal and the peak-trough observer have the same problem, in fact, when predictions are considered as a function of mean luminance. Note that, in either the middle or right panels of Fig. 3, the low-frequency end of each function is displaced only half a log unit downward from the function above it. However, the mean luminance changes by a log unit from one function to the next. In other words, at low temporal frequencies the observer is predicted to always show square-root (DeVries-Rose) behavior as a function of mean luminance. (The square-root behavior is predicted no matter what the deterministic filter is. Notice that the deterministic filter in Fig. 3 is predicting something closer to Weber's-law behavior.)

Human observers, however, only display square-root behavior over a limited range of mean luminances. They tend toward Weber's law at high mean luminances (particularly for low temporal frequencies) and towards linear behavior at low mean luminances (particularly for higher temporal frequencies).

Essentially the models always predict square-root behavior for the following reason. If the only noise source is early (before the gain control, as is true of quantal fluctuations), then the gain control always turns down the signal and noise by the same amount, and thus the gain control can produce no change in the observer's performance. If the only noise is early and it is quantal noise, then the behavior is predicted to always be square-root behavior. One will never get Weber's law at high mean luminances or linear behavior at low. This particular problem with including quantal fluctuations in a model has been commented on before (e.g. Barlow, 1965; Cohn & Lasley, 1986; Hood & Greenstein, 1990; Shapley & Enroth-Cugell, 1984; Sperling, 1989; Walraven & Valeton, 1984). Notice that this problem is quite analogous to the problem that the ideal observer has only the temporal frequency dimension.

DISCUSSION

Improving the predictions for flicker

As we saw above, when the only noise is quantal fluctuations, the predictions from the ideal observer rule will be wrong considered both as a function of temporal frequency and as a function of mean luminance. The predictions from the peak-trough decision rule, while more realistic as a function of temporal frequency, will be wrong as a function of mean luminance. These conclusions hold not only for the specific model shown in Fig. 3 but for all models of the class shown in Fig. 1.

Suppose one wanted to include quantal fluctuations in a model of temporal sensitivity at different mean luminances, however. To include them in a non-trivial way (that is, to make them responsible for a decrease of sensitivity that is proportional to the square-root of mean luminance under some conditions) requires solving three other problems.

(1) Something must be done to move the predicted behavior out of the square-root (DeVries-Rose) region into the Weber region at the appropriate luminances and frequencies. As mentioned above, a standard solution is to include late noise that dominates at relatively high mean luminances and particularly for low frequencies. (See, e.g. Shapley & Enroth-Cugell, 1984. This late noise needs to act in conjunction with a suitable deterministic filter that predicts Weber's law under the correct conditions. Once late noise is dominant, the observer's sensitivity by either decision rule will be controlled by the deterministic filter.)

(2) Something must also be done to produce the linear region that occurs in human psychophysical results. That is, at relatively low mean luminances, particularly at high temporal frequencies, amplitude threshold is unaffected by mean luminance. This can be accomplished by invoking more tailor-made early noise (e.g. dark/light) and/or tailor-made late noise. For example, Shapley and Enroth-Cugell (1984, p.294) suggest getting high-temporal frequency linearity by using late noise biased toward high temporal frequencies (in conjunction with a deterministic filter that shows high-temporal frequency linearity).

(3) A suitable decision rule must be used. It cannot be an ideal observer. Although that observer may seem most natural when thinking about quantal fluctuations as an unavoidable limitation imposed by the physical world, it does not predict realistic temporal filtering. Throughout the luminance range where quantal fluctuations dominate, the observer's predicted sensitivity will simply reflect the quantal noise spectrum.

Modifying the ideal observer to consider a constant number of cycles at each frequency (rather than the full stimulus which we are assuming was on for a fixed duration in seconds) will produce the desired results. But as will be discussed further below, it does not seem justifiable for the temporal case on the basis of known visual processes, although the analogous modification for the spatial case may be.

A peak-trough observer is a good candidate. This, unfortunately, may seriously hinder efforts to have a practical computable model of the dynamics of light adaptation because extensive use of Monte Carlo techniques will often be required. In some situations it can be adequately approximated by use of the pooling formula suggested by Quick (1974) and explored since then by a number of investigators (see Graham, 1989, Chap.6).

Spatial frequency is different

Using a model in which there are only quantal fluctuations, low-level visual processes, and an ideal observer, Banks, Geisler and Bennett (1987, Fig. 2; also see Fig. 13 in Geisler, 1989), predict a reasonably shaped high-spatial-frequency decline. We, however,

failed to get a reasonably shaped high-temporal-frequency decline using a similar approach (e.g. Fig. 3 right panel). The question naturally arises: what did Banks *et al.* do differently? As is discussed further below, the answer is twofold. First, the lower-level visual mechanisms in their approach include receptor aperture and optical blur. Such preneural processes are intrinsically different from the temporal filtering in our model (and from spatial neural filtering as well). Second, the sinusoidal stimuli in their study contain a constant number of cycles at all spatial frequencies rather than being of constant extent.

Pre-neural factors (optical blur, receptor aperture). The receptor aperture directly integrates light ("counts quanta") over some area. This integration contributes slightly to the high-frequency decline in the visible spatial frequency range. However, since there is no fixed physical temporal aperture to a receptor (no "shutter"), this kind of effect cannot contribute at all to a high-temporal-frequency decline.

Optical blur produces a substantial amount of the high-spatial-frequency decline in the Banks *et al.* (1987) calculation. However, in spite of what one might think at first, optical blur is not (particularly not in the context of an ideal observer) a spatial filter analogous to the temporal filter in our model. Nor, in fact, is optical blur analogous to the spatial filtering produced by receptive fields. Optical blur attenuates the contrast of high spatial frequency gratings more than of low spatial frequency, but optical blur does not change the amount of high-spatial-frequency content in the quantal noise (quite unlike the filtering stage in Fig. 3 which attenuates the noise as much as the signal). For, after the light has gone through a lens and been blurred, it is still light. Light (except in some extremely unusual circumstances) is a Poisson process—that is, the probabilities of quanta occurring at different points in time and space are independent of one another. Thus, although optical blur rearranges the average value of photons coming from sinusoidal gratings in a way that attenuates the contrast of high spatial frequency gratings more than of low spatial frequency gratings, it does not introduce correlations among neighboring points, and thus it does not attenuate the amount of high spatial frequency content in the quantal noise.

The temporal filtering in our model and the kind of spatial filtering produced by receptive fields act quite differently from optical blur. Like optical blur, they do attenuate the (average) contrast at high temporal or spatial frequencies more than at low. But in so doing they introduce correlations between responses at different points in time or space. To see this, consider the following. Consider a moment when there happens to be an unusually large number of photons caught by one receptor (relative to the average expected). This unusual event is guaranteed to produce unusually large responses from several neurons (those having receptive fields containing the one receptor) at several moments in time (all the moments in time through which the response from the first moment lasts). These resulting correlations

across neurons and across times change the characteristics of the noise itself. Indeed the correlations attenuate the high frequency content (relative to the low) in the noise to the same extent as the filter attenuated high frequency signals. Thus, the fact that optical blur contributed to the high-spatial-frequency decline of Banks *et al.* (1987) does not mean that spatial and temporal "neural" filtering like the deterministic stage in Fig. 1 can contribute to either a high-spatial or a high-temporal-frequency decline.

Constant number of cycles in the stimuli. The sinusoidal stimuli used by Banks *et al.* contained the same number of cycles regardless of frequency, and the height of the grating equaled the width. Thus, stimulus area was inversely proportional to the square of spatial frequency. As is well known, the effectiveness of quantal fluctuations is inversely proportional to the square-root of the area considered by the ideal observer (e.g. Barlow, 1958). Thus, for the stimuli of Banks *et al.*, the effectiveness of the quantal fluctuations for an ideal observer will be directly proportional to spatial frequency. To put it another way, for these stimuli and the ideal observer, the effective spectrum of the quantal noise is not flat as in Fig. 3, but *increases* in proportion to frequency. Consequently, for these stimuli (in the absence of the other preneural factors), the ideal observer's sensitivity will *decline* in proportion to spatial frequency (that is, the high-spatial-frequency decline will have a slope of -1 on log-log coordinates). This represents the second substantial contribution to the high-spatial-frequency decline predicted by Banks *et al.* The analogous choice of flickering stimuli with a constant number of cycles would produce an analogous high-temporal-frequency decline in the predictions of an ideal observer (but with a slope of $-\frac{1}{2}$ rather than -1 since the temporal stimulus has only one dimension of extent while the spatial had two). While not steep enough to be consistent with psychophysical flicker results, it would certainly be better than the predictions in Fig. 3.

Banks *et al.*, justify their choice of stimuli on the basis of psychophysical results showing that, as the number of cycles in a grating is increased, the human observer's sensitivities continue to improve only for a limited number of cycles. And that limit is about the same for all spatial frequencies and about the same both perpendicular to and parallel to the bars. The ideal observer on the other hand continues to improve indefinitely as more area is added. Thus the ideal observer cannot possibly be correct for large number of cycles; some other factor is limiting performance at large number of cycles. In an attempt to minimize this other factor ("neural summation"), they choose stimuli of constant number of cycles. Indeed, they discuss the case of stimuli of constant extent and point out that their approach could not predict the shape of the high-spatial frequency decline for those stimuli (see, e.g. Geisler, 1989, p.287). Their use of a restricted set of stimuli is consistent with the overall goals of their investigation, one of which is to explore the stimulus realms where the ideal observer and quantal fluctuations might be the limiting factor. But for our

purposes it is not sufficient to make predictions correctly for one set of stimuli only (those with constant numbers of cycles); we also need the predictions to be correct for others (e.g. for those for constant extents) if we are to have a computable model for arbitrary stimuli.

Modifying the ideal observer to consider a constant number of cycles. The fact that, in psychophysical results, sensitivity increases up to a fixed number of cycles regardless of frequency and the success of the Banks *et al.*, predictions for constant-number-of-cycles stimuli suggest a modification of the ideal observer. This modified ideal observer is one that is ideal except that it can only consider some fixed number of cycles no matter what the extent or frequency of the stimulus; in other words, the extent it considers varies inversely with frequency. (Such a suggestion is reminiscent of the suggestion of different summation areas for different spatial or temporal frequencies that was made in a related context by van Nes, 1968; van Nes & Bouman, 1967; van Nes *et al.*, 1967.)

But does the suggestion above make any sense in terms of mechanism or is it merely an *ad hoc* rescue of the model by specifying an odd decision rule? One can make some sense of this suggestion for the spatial frequency dimension but justification is more difficult for the temporal frequency dimension, and on neither dimension can it completely rescue the ideal observer. To make sense of this suggestion, one might start by expanding the framework in Fig. 1 to include multiple frequency-selective channels acting in parallel rather than a single channel as shown there. (These channels would be spatial frequency or temporal frequency selective depending on which case one has in mind.) Then one can postulate that the bandwidths of the channels are all equal in logarithmic frequency, that is, the weighting functions characterizing the different channels all have the same number of cycles and thus have extents that vary inversely with frequency (or frequency-squared if one considers both dimensions in the spatial case). With such a model, even with stimuli of a constant spatial or temporal extent, this ensemble of multiple channels might act very much as if they were stimuli of a constant number of cycles (with some caution—see next paragraph). For spatial frequency, there is compelling psychophysical evidence that frequency selective channels exist and further that their bandwidths are all much the same in logarithmic frequency. The available psychophysical evidence suggests, however, that temporal frequency selectivity is much less than spatial frequency selectivity. (The evidence is reviewed in Graham, 1989, Chap.12). While there may be a small number of different channels on the temporal frequency dimension, they are much more broadly tuned than those on the spatial frequency dimension and they would probably not be effective in the role envisioned for them here.

However, even if there are multiple channels, it is not possible to adequately model human psychophysical results with an ideal observer. For, as mentioned above, an ideal observer (limited only by noise that is homogeneous across space or time) would continue to show

substantial improvement in sensitivity as the number of cycles in a stimulus of a particular frequency was increased even beyond that number of cycles included in the weighting function. Human observers do not show such a dramatic increase in sensitivity although they do show a lesser one (see below). This again is reason for concluding that, if one wants a computable model that one can use to predict the responses to arbitrary stimuli, one cannot use an ideal observer unless one postulates noise with specific qualities.

On the other hand, the spatial pooling results are another good reason for considering the use of a peak-trough observer. For, while not showing as much improvement with increasing spatial extent as predicted by an ideal observer, human observers do show some increased summation as number of cycles is increased, and the amount they show is consistent with that predicted by retinal inhomogeneity and a peak-trough observer (e.g. Robson & Graham, 1981; Graham, 1989, Chap.6).

Conclusion

Of course quantal fluctuations exist as a source of noise in the visual stimulus, and we accept the ideal observer's usefulness as a benchmark for visual behavior. However, within the framework in Fig. 1, predictions like those in Fig. 3 lead us to the following tentative conclusion. Either the source of noise limiting human sensitivity is almost always noise other than quantal fluctuations and/or the ideal observer is the wrong decision rule to describe actual visual processing.

There seems no compelling reason to believe that quantal fluctuations with or without an ideal observer are an important factor in understanding the effects of light adaptation on the visual performance of humans. In Geisler *et al.*'s calculations for example, although the predictions from a model incorporating quantal fluctuations, pre-neural factors, and an ideal observer, parallel the human psychophysical thresholds, the human results are at least a factor of 5 and often a factor of 20 less sensitive than the predicted (see, e.g. Geisler, 1989). Hood and Greenstein (1990) concluded that adding quantal noise as a limiting factor on rod sensitivity produced implausible predictions for changes in the rod system with some diseases. Pelli (1990, p.16) does suggest tentatively that absorbed-photon noise can account for the observer's equivalent noise at most spatiotemporal frequencies. His conclusion depends on several assumptions however, and on one particular psychophysical task. Until those assumptions and that task are evaluated further, the weight of the evidence is against quantal noise as a limiting factor on performance. (Quantal fluctuations may, of course, have played a role in the course of evolution.)

Therefore, for many purposes, quantal fluctuations and other probabilistic processes might be ignored entirely and the output of a deterministic stage computed (e.g. the left panel Fig. 3). Of course, getting a deterministic stage to exactly mimic sensitivity as a

function of temporal frequency and mean luminance is not trivial. Several candidates exist in the literature, however, in addition to the feedback module used here. Sperling and Sondhi (1968) used a combination of feedback, feed forward (and linear lowpass) to obtain rather successful predictions although one that has some trouble at low temporal frequencies. More recently, Tranchina and Peskin (1988) have produced two different nonlinear models whose output can be computed for arbitrary input functions of time. Perhaps one of these deterministic stages would be a satisfactory model for some purposes.

The question of the role of quantal fluctuations in limiting human vision is still not settled. It is safe to say, however, that if one wishes to incorporate them into a model of temporal vision that can be applied to arbitrary stimuli, one cannot do so without appropriate attention to a number of other features in the model. Also, it would be unwise to cavalierly invoke them as an explanation for the apparent square-root behaviour seen in some psychophysical results.

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