Photon and cortical noises limit what we see

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SUMMARY: Random fluctuations arise at every stage of visual processing, but does this noise restrict what we see? Adapting a technique developed by radio and television engineers in the 1940's, we measure the effect of added visual noise on grating and letter identification, and estimate the amount of added noise that is equivalent to the observer's intrinsic noise. We map out the equivalent noise as a function of the signal size, duration, and luminance, and compare our measurements to the predicted equivalent noise of several intrinsic noises arising at various levels in the visual system. The results show that visual sensitivity is limited by the sum of photon and cortical noises, each dominating a distinct stimulus domain. The visibility of small brief dim signals is limited by photon noise, while the visibility of large prolonged bright signals is limited by cortical noise. The boundary separating photon and cortical noise domains is a critical amount of light within the stimulus: the product of luminance, area, and duration. In the photon-noise domain, the measured equivalent noise tells us that vision uses only 2% of the light entering the eye. The cortical equivalent noise is self-similar, and scales with luminance, size, and duration, affirming suggestions that cortical processing is scale-invariant. In brighter light, we can see smaller, briefer, and fainter objects, but, even in the brightest light, we will never see an edge whose two sides differ by less than 1% in luminance, the faintest that the cortical neurons can detect in their own noise. These two noises, photon and cortical, largely account for the sensitivity of achromatic photopic foveal vision. Correlated noise may dominate physiological recordings while hardly affecting psychophysical threshold, underscoring our comparison of these psychophysical estimates with recordings from V1 neurons (Lin et al. 2015; Goris et al. 2014).

We present psychophysical data bearing on a key property of the neural system that does vision. Noise limits information transmission: what can be seen. Four physical and physiological sources of noise are considered, and all but two are rejected as inconsistent with the data. The remaining photon and cortical noises have very simple models yet fit very well. We show that the cortical neural noise dominates for smaller briefer dimmer targets, and we compare it to physiological recordings.

Human vision is a complex biological system and has nonlinearities lurking in every corner. Perceptual decisions such as object recognition are necessarily nonlinear. However, applicability of the equivalent noise technique does not require that the individual components behave linearly. The equivalent noise technique models the input-output behavior of the system as a whole. Under our conditions, measurements of threshold signal energy as a function of the added white noise level always follow linear relationship displayed in Fig. 1a,

$$E \propto N + N_{eq} \qquad (1)$$

where E is the threshold energy, N is added display noise, and N_{eq} is internal noise in the visual system. That linear input-output relationship (the additive effects of noise on threshold energy) is all we need to apply the equivalent noise technique. The psychophysically measured equivalent input noise is predicted to be the sum of the equivalent input noises of the various sources,

$$N_{eq} = N_{thermal} + N_{photon} + N_{ganglion} + N_{cortical} \qquad (2)$$

Eq. 2 is our model, the sum of four noises. However, only two of the noises matter (the others don't explain any of our data), so the other two terms were dropped, reducing Eq. 2 to

$$N_{eq} = N_{photon} + N_{cortical} \qquad (3)$$

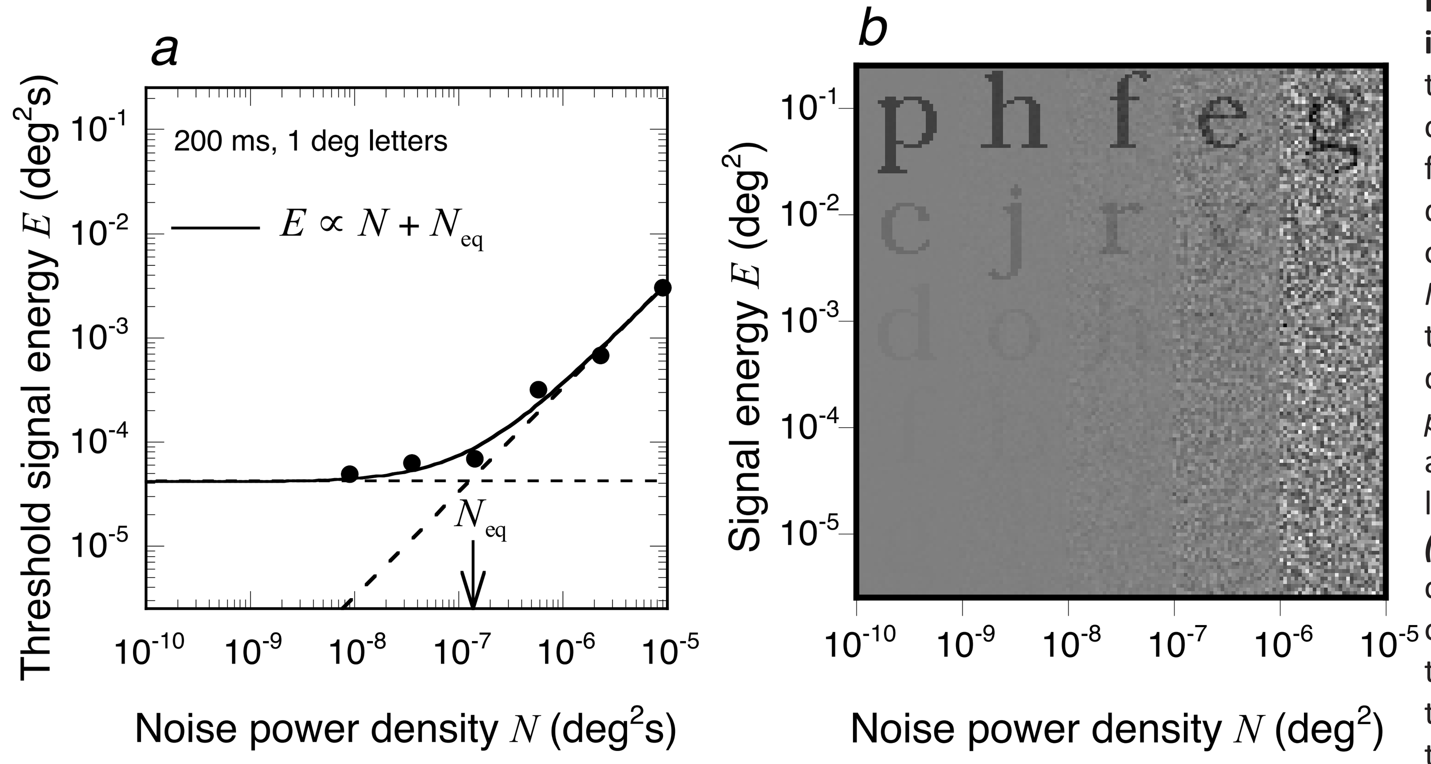

Fig. 1. Measuring the observer's equivalent input noise. We tested letters and gratings; this figure is for letters. ***(a)*** Dynamic. Signal contrast energy E at threshold (64% correct) for identifying letters on a background of dynamic visual noise is plotted as a function of the display-noise power spectral density N. The good fit provided by Eq. 1 shows that threshold signal energy depends linearly on display noise N, where the *equivalent input noise* N_{eq} is a fitted constant. The curve asymptotically approaches the two dashed lines (slopes 0 and 1), which intersect at N_{eq}. ***(b)*** Static. You can use this letters-in-noise chart to test your own vision at a distance of 40 cm. You will find that the faintest identifiable letters trace out a curve similar to that plotted in *a*. The noise level at which the curve turns up is your static equivalent input noise for letters of this size. Contrast power is dimensionless.

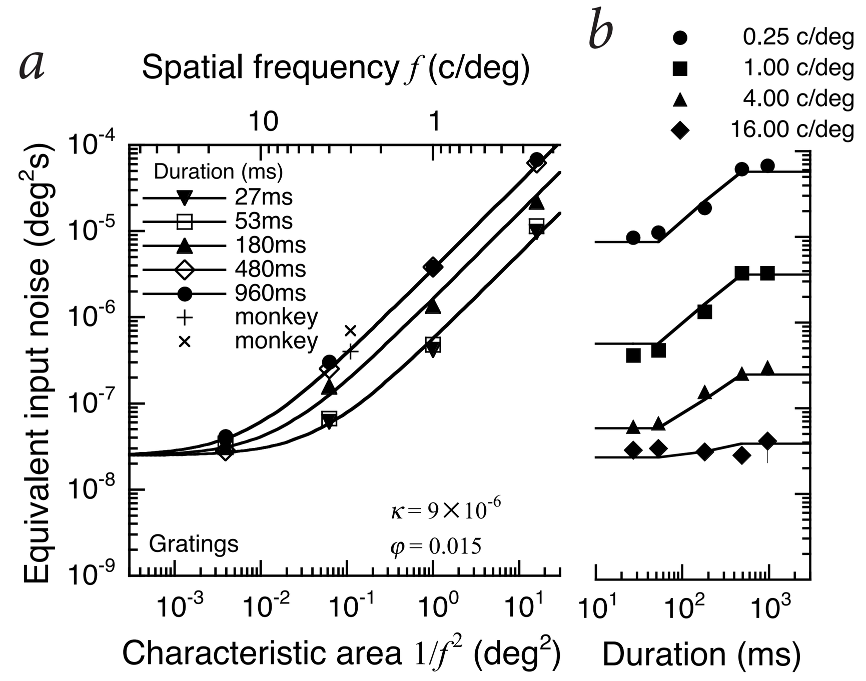

Fig 2. Equivalent noise as a function of signal area and duration. The human data points have been fit by Eq. 3 (solid lines). These are results for gratings; similar results for letters are not shown. **(a)** The measured equivalent input noise for identifying gratings is plotted as a function of characteristic area. The bottom and top scales show the letter size and grating spatial frequency, respectively. Observer MR. The + and × in panel b are for a monkey neuron (courtesy of AJ Movshon). **(b)** The same data are plotted as a function of signal duration. Three other observers (WT, CF, BS) produced similar results, not shown here. For each task, all the measured values are well fit by Eq. 3 (solid line), with just two degrees of freedom, the magnitudes of the photon and cortical noises, controlled by parameters κ and φ. The figure displays observer MR's results fit by Eq. 3, and the values of the fitted parameters and . Letter size is the typographic "x height", i.e. the height of letters, like "x", with no ascender or descender. Characteristic area, the horizontal scale, is one square period of the grating. Equivalent input noise was measured for 0.25, 1.25, 7.4, and 35 deg letters, and 0.25, 1, 4, and 16 c/deg gratings at signal durations ranging from 27 to 960 ms.

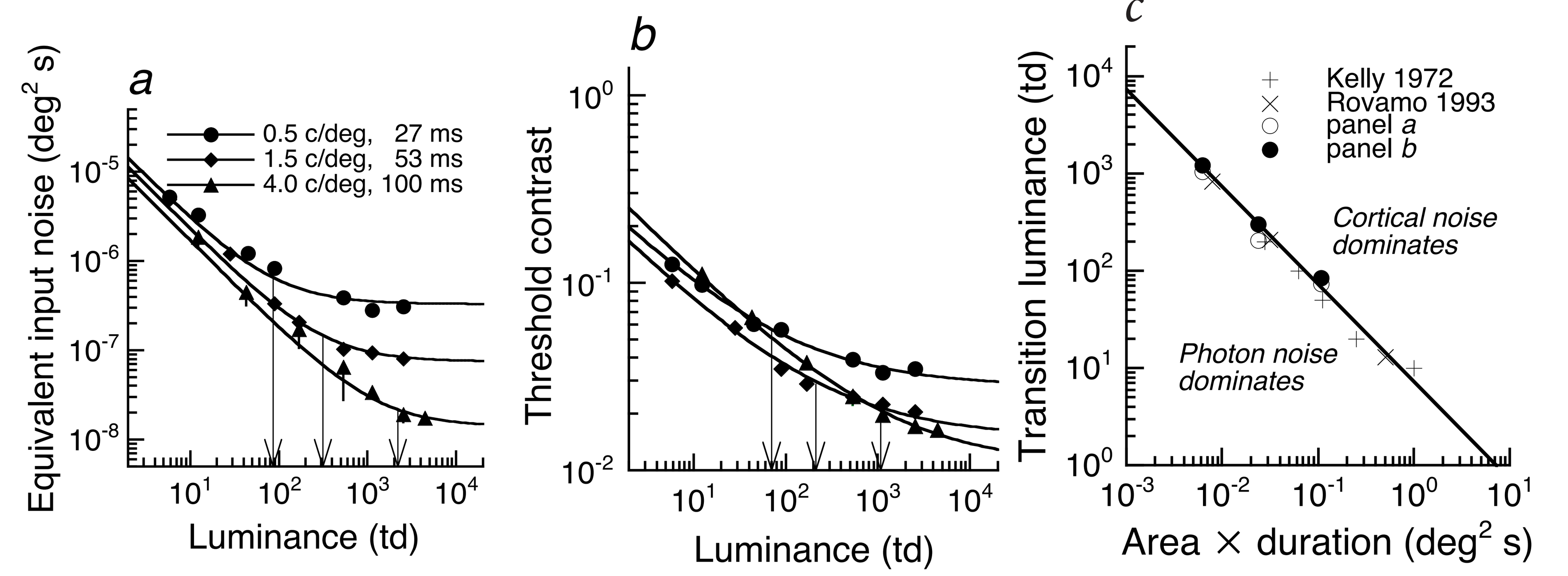

Fig. 3. Effect of luminance. (a) Equivalent input noise and **(b)** threshold contrast plotted as functions of the luminance for the grating identification task. Spatial frequency and duration of the signal are indicated in *a*. Viewing was monocular, through a 2 mm artificial pupil. Panel *a* includes three downward error bars showing one standard deviation across repeated measurements with the same observer. **(c)** Past authors have noted the difference between Rose-Devries and Weber slopes of threshold functions, as a function of luminance, and called it the "transition" luminance. Here we estimate it as the luminance at which $N_{photon} = N_{cortical}$, for each value of AT, the area×duration of the grating, where $A=f^{-2}$. The -1 slope line represents LAT =7.5 td deg^{2}s = 200,000 photons transduced, where L is luminance, A is signal area, and T is signal duration. Grating identification is photon-noise-limited below the line, and cortical-noise-limited above it. The open and filled circles are the transition luminance estimates from panels *a* and *b*, and the + and × are estimates based on published graphs of threshold vs. luminance. van Nes et al. showed evidence, with static gratings, that the transition luminance is proportional to A^{-1}.

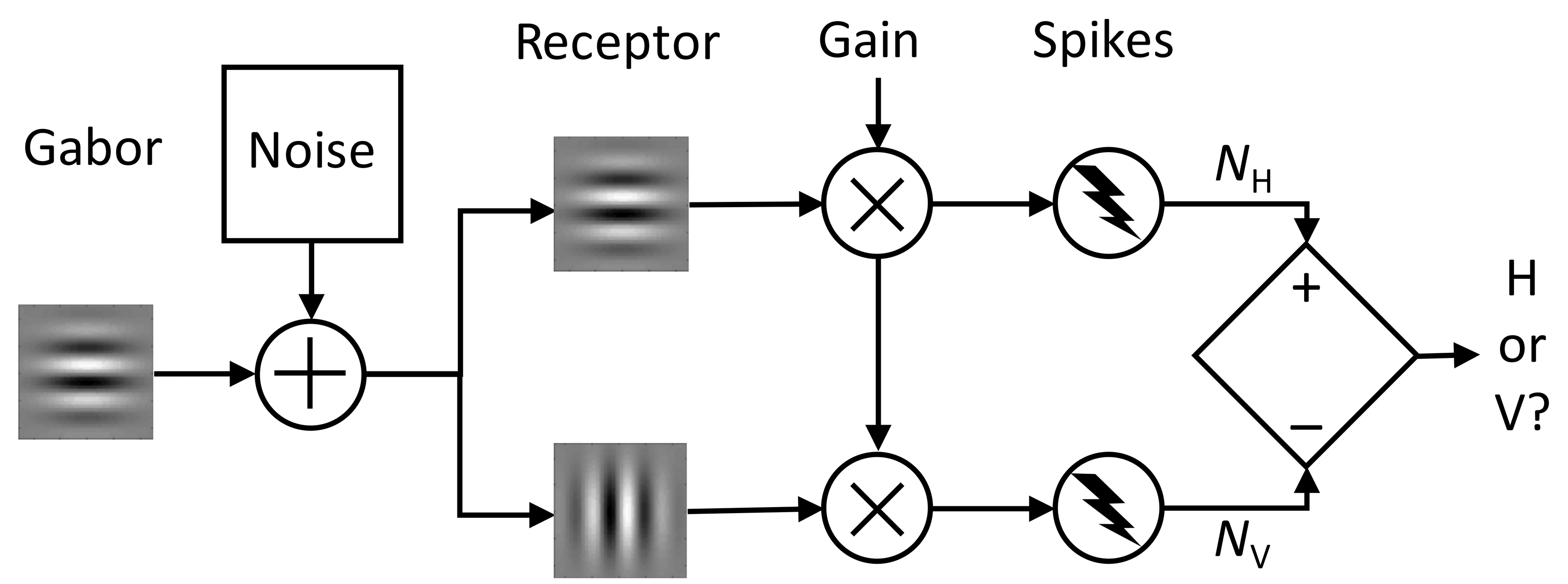

Fig. 4. Orientation discrimination in visual noise by the neural noise model of Goris et al. (2011) and Lin et al. (2015) for V1. The stimulus S consists of a horizontal or vertical Gabor, plus white noise. Both articles attribute most of the physiologically measured variance to a variable gain G which is shared by all neurons locally and changes randomly from trial to trial: $G \sim \mathrm{Gamma}(1/\sigma_G^2, \sigma_G^2)$, where σ_G^2 is the variance of the gain G. The receptor input, scaled by this gain drives a Poisson spike generator, which emits N spikes: $N \sim \mathrm{Poisson}(G\, f(S)\, t)$.

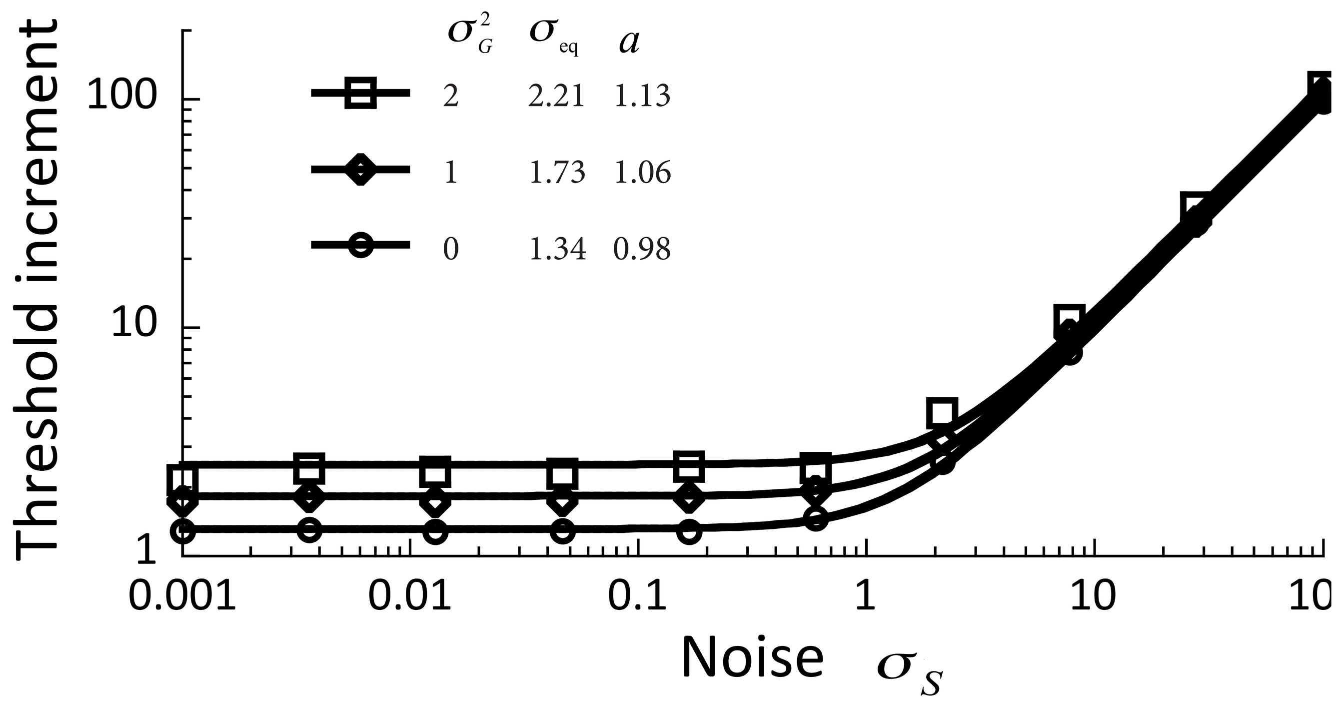

Fig. 5. Threshold for orientation discrimination of the neural model in Fig. 4. The model was implemented in software. On each trial, only one receptor receives signal, producing a mean increment in number of spikes, and all the receptors receive noise. As with human observers, we measured threshold for many noise levels, and then fit a function to the results: $\Delta = a\sqrt{\sigma_S^2+\sigma_{eq}^2}$ where Δ is the increment (mean spikes) produced in the receptor that is sensitive to the signal, a is a proportionality constant, σ_S is the standard deviation of the added noise, in spikes, like the increment, and σ_{eq} is the equivalent input noise of the neural model for this task. The gain variance has surprisingly little effect on the discrimination threshold and the equivalent noise estimate. We tested gain variances ranging from zero to 2, corresponding to a Fano factor of zero to 2. Common-mode noise tends to be discounted by a decision based solely on comparing similarly affected receptors. Thus the equivalent noise mostly reflects the Poisson variance, and is approximately the mean spike rate scaled by the gain.

Thus the cortical equivalent noise measured psychophysically may reflect the spike rate of the cortical neurons mediating the perceptual task at threshold.

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