Noise Frame Duration, Masking Potency and Whiteness of Temporal Noise

Heljä Kukkonen,[1] Jyrki Rovamo,[1] Kristian Donner,[2] Marja Tammikallio,[2] and Antti Raninen[2]

Purpose. Because of the limited contrast range, increasing the duration of the noise frame is often the only option for increasing the masking potency of external, white temporal noise. This, however, reduces the high-frequency cutoff beyond which noise is no longer white. This study was conducted to determine the longest noise frame duration that produces the strongest masking effect and still mimics white noise on the detection of sinusoidal flicker.

Methods. Contrast energy thresholds (E_{th}) were measured for flicker at 1.25 to 20 Hz in strong, purely temporal (spatially uniform), additive, external noise. The masking power of white external noise, characterized by its spectral density at zero frequency N_0, increases with the duration of the noise frame.

Results. For short noise frame durations, E_{th} increased in direct proportion to N_0, keeping the nominal signal-to-noise ratio [$SNR = (E_{th}/N_0)^{0.5}$] constant at threshold. The masking effect thus increased with the duration of the noise frame and the noise mimicked white noise. When noise frame duration and N_0 increased further, the nominal *SNR* at threshold started to decrease, indicating that noise no longer mimicked white noise. The minimum number of noise frames per flicker cycle needed to mimic white noise decreased with increasing flicker frequency from 8.3 at 1.25 Hz to 1.6 at 20 Hz.

Conclusions. The critical high-frequency cutoff of detection-limiting temporal noise in terms of noise frames per signal cycle depends on the temporal frequency of the signal. This is opposite to the situation in the spatial domain and must be taken into consideration when temporal signals are masked with temporal noise. (*Invest Ophthalmol Vis Sci.* 2002;43:3131–3135)

Adding white temporal noise to a temporal signal allows the investigation of "central" aspects of temporal contrast detection beyond the initial optical, retinal, and neural filtering,[1–4] analogous to experiments on spatial vision.[5–7] With strong external noise, the contrast energy at detection threshold increases in proportion to spectral density of the noise. When a stimulus (signal plus noise) is transferred through the visual system, early filtering attenuates signal and noise contrast similarly without affecting the signal-to-noise ratio (*SNR*), as long as the masking effect of the external noise remains stronger than that of the internal noise.

The masking power of external noise is described by its spectral density. The spectral density of white spatiotemporal noise is the product of the spatial dimensions of the noise checks, duration of each noise frame, and root mean square (RMS) contrast of noise squared.[6,8] Spatial parameters are held constant for purely temporal noise, and its spectral density can be expressed simply as the product of the duration of the noise frame and RMS contrast squared.[1,2,9] The masking effect of white temporal noise is thus dependent on its contrast and the duration of each noise frame.

The frame rate of the display limits the temporal bandwidth of noise. Hence, so-called white noise always has a specific high-frequency cutoff, beyond which it is no longer white. Previous research indicates, however, that noise reduces detectability only at the frequencies of the signal and its immediate neighborhood.[8,10,11] Regardless of whether the detection mechanism is a filter matched to the signal[1] or consists of channels tuned to different temporal frequencies,[3,4] the variation of noise is thus relevant only at the frequencies of the matched filter or within the channel detecting the signal. This means that as long as the noise power spectrum is "flat" over the frequency range of the filter or channel detecting the signal, noise can be regarded as white. This seems to be the case both in spatial[10–12] and temporal[2] vision.

When investigating pathologic vision with reduced flicker sensitivity or detection of low or high temporal frequencies at which flicker sensitivity is low, high signal contrasts have to be used together with high spectral density of external noise. Because of the limited contrast range, the noise-masking effect is then increased by increasing the duration of the noise frame. This, however, lowers the high-frequency cutoff (see Kukkonen et al.[10]), and a limit will be reached at which the white noise bandwidth no longer fully covers the temporal frequency spectrum used for signal detection.

In the present study, we determined the lowest high-frequency cutoff—that is, the minimum bandwidth of temporal noise that still acts as white in masking sinusoidal flicker (1.25–20 Hz) by determining the longest noise frame duration that still mimics white noise.

Methods

Stimuli were generated under computer control on a 16-in. red-green-blue (RGB) monitor (Flexscan T57S; EIZO Nanao, Cypress, CA) with Fast Phosphor P22 used in white mode and driven by a graphics board (Millennium II Powerdesk; Matrox, Dorvoli, Montreal, Canada) that generated 640 × 480 pixels, each 0.47 × 0.47 mm^2 in size. The frame rate of the monitor was 132 Hz. The amplitudes and frequencies of flickering stimuli were checked with a phototransistor (TIL81; Texas Instrument, Dallas, TX). No attenuation of amplitude was measured at 30 Hz. Even if there were any contrast attenuation at shorter noise frame durations (down to 1/132 seconds), signal and noise are similarly affected at each temporal frequency so that *SNR* remained unchanged.

The average luminance of the display was 50 cd/m^2. To increase the number of gray levels available, the red, green, and blue outputs of

From the [1]Department of Optometry and Vision Sciences, Cardiff University, Cardiff, Wales, United Kingdom; and the [2]Department of Biosciences, University of Helsinki, Helsinki, Finland.

Supported by Grants 36154 and 49947 from the Academy of Finland.

Submitted for publication September 7, 2001; revised March 18, 2002; accepted April 3, 2002.

Commercial relationships policy: N.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

Corresponding author: Jyrki M. Rovamo, Department of Biosciences, Division of Animal Physiology, PO Box 65, University of Helsinki, FIN-00014 Helsinki, Finland; rovamo@cardiff.ac.uk.

the graphics board were combined by means of a video summation device.[13] The luminance response of the monitor was linearized by gamma correction. For further details, see Rovamo et al.[2]

Stimuli

The sinusoidally flickering signal was a sharp-edged circular field 8 cm in diameter. A black cardboard mask limited the equiluminous surround to a circular area 20 cm in diameter. Viewing distance was constant at 115 cm, producing a foveal stimulus 4° in diameter within a surround of 10° in diameter.

Flicker was produced by changing the color look-up table of the graphics board during each vertical retrace period of the display. The total duration of the signal was 2.4, 2, 1, 0.5, and 0.25 seconds at 1.25, 2.5, 5, 10, and 20 Hz, respectively. The number of cycles displayed was thus five cycles for 2.5- to 20-Hz signals. To keep the exposure time and experiment duration reasonable, only three cycles were displayed at 1.25 Hz.

Spatially uniform purely temporal noise with the widest temporal bandwidth was produced by adding a random luminance to the signal at each frame of the display lasting 7.5 ms. The duration of the noise frame was increased by allowing this random increment or decrement to last for several frames. The longest noise frame duration was 545 ms (72 frames) at 1.25 Hz, 455 ms (60 frames) at 2.5 Hz, 227 ms (30 frames) at 5 Hz, and 167 ms (22 frames) at 10 and 20 Hz. At all noise frame durations, the signal luminance varied in every display frame according to the sinusoidal waveform.

The random luminances producing the noise were drawn independently from a Gaussian luminance distribution with zero mean and truncation at ±2.5 SD units. The RMS contrast of temporal noise was 0.15, except at 1.25 Hz (0.25, subject AR; 0.20, subject MT). These contrasts were chosen so that external noise always limited detection. At all flicker frequencies the contrast energy threshold measured with the lowest spectral density of external white noise was always more than 10 times higher than the threshold measured without added noise—that is, when internal neural noise limited detection.

The contrast energy of the flickering signal was calculated by numerical integration across time[6] as

$$E = \Sigma c_t^2 \Delta t, \tag{1}$$

where $c_t = [L_t - L_0]/L_0$, L_t is the temporal contrast waveform, L_0 is average luminance, and Δt is the nominal duration of each temporal frame of the display—that is, 1/132 seconds.

The power spectrum of temporal noise is given by[6]

$$N_f = c_n^2 \Delta t_n [\sin(\pi f \Delta t_n)/(\pi f \Delta t_n)]^2 \tag{2}$$

where f is the temporal frequency, c_n is the RMS contrast of noise, and Δt_n is the duration of each noise frame. At low temporal frequencies, at which noise is white and the spectral density of temporal noise is the same as at zero frequency N_0, equation 2 reduces to[10]

$$N_0 = c_n^2 \Delta t_n \tag{3}$$

Equation 3 shows that increasing the duration of the noise frame increases the spectral density of temporal noise at zero frequency and within the white bandwidth of noise. The temporal frequency at which the spectral density of noise starts to decrease—that is, noise ceases to be white—is consequently reduced. Above this corner frequency $(2\Delta t_n)^{-1}$ the average power spectrum begins ringing, according to the Fourier spectrum of a sinc function of equation 2. For a graphical presentation of the relationship between N_0, noise frame duration, and cutoff frequency, see the spatial equivalent.[10]

$$SNR = [E_{th}/N_0]^{0.5} \tag{4}$$

where E_{th} is contrast energy at detection threshold. The data were modeled by

$$SNR = SNR_{max}[1 + (n/n_c)^5]^{-k} \tag{5}$$

where SNR is the nominal signal-to-noise ratio at threshold, n is the noise frame duration in cycles, n_c is the critical noise frame duration at which SNR started to decrease, and $-5k$ is the slope of decrease of SNR. The exponent 5 was chosen to model the sharp transition from constant SNR_{max} to decreasing SNR shown by the data in Figure 1.

Procedures

Detection thresholds were measured in a dark room with the monitor as the only light source. Viewing was monocular. The pupil was dilated to 8 mm with 1 to 4 drops 10% phenylephrine hydrochloride (Metaoxedrine; Smith & Nephew Pharmaceutics Ltd., Romford, UK), leaving accommodation unaffected. Fixation was directed to the center of the stimulus field.

Thresholds were determined by a two-alternative forced-choice algorithm at the probability level of 84% correct (see Mustonen et al.[14]). Each trial consisted of two exposures of equal duration indicated by a sound signal. The two exposures contained different samples of noise, but only one exposure contained the signal. The subject's task was to indicate which exposure contained the signal by pressing one of two chosen keys on a computer keyboard. Auditory feedback was provided.

The threshold contrast was calculated as the arithmetic mean of the last eight reversal contrasts. Every data point shown is the median of three to five thresholds measured. For three to five threshold measurements, the median is more robust than the mean in estimating the true threshold, because the median is less affected by occasional outlying values.

Subjects

Two experienced subjects (aged 51 and 43 years) with normal vision participated in the experiments. AR was an uncorrected hypermetrope and MT was a corrected astigmatic myope (−0.50/−0.50 ax 80). Both had visual acuity of 6/5. Psychophysical data for subjects with normal vision tend not to vary from one subject to another more than the normal variation within each subject's data (as in the current experiments). It is, therefore, an accepted practice to use just two to three subjects to represent the normal performance of a healthy visual system.

The tenets of the Declaration of Helsinki were observed, and informed consent was obtained from both subjects before the experiments were conducted.

Results

In Figure 1, $[E_{th}/N_0]^{0.5}$ (the nominal SNR at threshold) is plotted as a function of the duration of the noise frame, expressed as a fraction of a flicker cycle. The results of the two subjects are practically identical. At all frequencies, there was an initial range of short noise frame durations at which the nominal SNR at threshold remained constant, indicating that E_{th} (not shown) rose in direct proportion N_0. Because N_0 is directly proportional to noise frame duration and represents the spectral density of external noise at the temporal frequencies at which noise is white, the result implies that the detection-limiting noise indeed grew proportionally to N_0, and that the external noise was dominant and effectively white within the detection filter, despite the decreasing bandwidth of noise.

With further increase in duration of the noise frame, the nominal SNR started to decrease at all temporal frequencies. The decreasing nominal SNR means that the spectral density of external noise at some frequencies affecting signal detection started to decrease, increasing the *true SNR* within the detec-

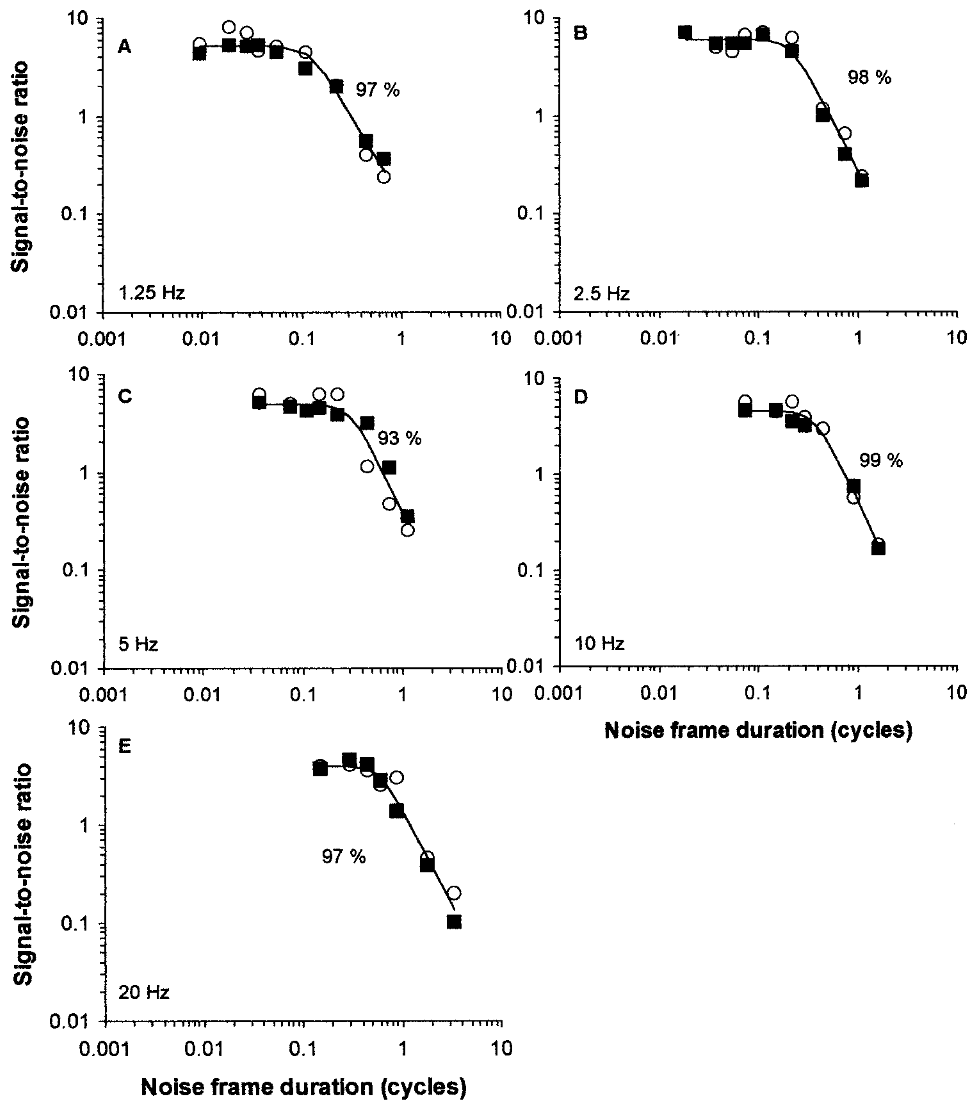

FIGURE 1. The nominal *SNR* at detection threshold, $[E_{th}/N_0]^{0.5}$, plotted as a function of duration of the noise frame expressed as a fraction of a flicker cycle. N_0 increased from 0.47 to 34.1×10^{-3} seconds at 1.25 Hz in subject AR; from 0.30 to 21.8×10^{-3} seconds at 1.25 Hz in MT; and from 0.17 to 10.2×10^{-3} seconds at 2.5 Hz, from 0.17 to 5.11×10^{-3} seconds at 5 Hz, and from 0.17 to 3.75×10^{-3} seconds at 10 and 20 Hz in both subjects. (**A**) through (**E**) correspond to flicker frequencies 1.25, 2.5, 5, 10, and 20 Hz, as indicated. (■) Subject AR; (○) subject MT. The critical noise frame duration is obtained by the least-square fit of equation 5 to the data in each panel. The goodness of fit[10] is shown in each panel.

tion filter, despite the continuing increase in N_0. The slopes of decrease of the nominal *SNR* ranged from −1.7 to −2.2. They are similar to slopes found previously in spatial experiments,[10] probably reflecting the decrease in effective noise within the frequency range used for detection. Ultimately, for long enough noise frame durations, internal neural noise would become dominant, and E_{th} would settle at a constant level. However, this situation (*SNR* slope of −0.5) was not reached within the range of frame durations used.

The continuous line is the least-square fit of equation 5 to the data in each panel (Fig. 1). The critical duration (n_c) refers to the point at which *SNR* started to decrease, thus marking the longest noise frame duration that still mimicked white noise. The n_c values determined from the least-square fit (±95% confidence intervals) were 0.12 ± 0.02, 0.22 ± 0.03, 0.30 ± 0.06, 0.37 ± 0.03, and 0.62 ± 0.09 cycles, corresponding to 96, 88, 60, 37, and 31 ms for flicker frequencies 1.25, 2.5, 5, 10, and 20 Hz, respectively.

In Figure 2A, (n_c) is plotted as a function of flicker frequency (f). Because log n_c increased more or less linearly with log f, n_c was described by $n_c = af^b$, where a and b are constants. The best fit of this equation to the data were achieved with $a = 0.10$ and $b = 0.58$.

The inverse of n_c indicates how many noise frames are needed within each flicker cycle for mimicking white noise. The values of $1/n_c$ for the five flicker frequencies used (in increasing order) are 8.3, 4.5, 3.3, 2.7, and 1.6 noise frames per signal cycle. The relative cutoff frequency f_c of the noise spectrum[10] was obtained as $f_c = (2n_c)^{-1}$; which gives f_c = 4.2 ± 0.7, 2.3 ± 0.3, 1.7 ± 0.3, 1.4 ± 0.1, and 0.8 ± 0.1 times the flicker frequency, for 1.25, 2.5, 5, 10, and 20 Hz, respectively. As n_c is expressed in cycles, f_c is a factor that indicates how much higher (or lower) in comparison with the flicker frequency the cutoff frequency of noise must be to mimic white noise.

The absolute cutoff frequency (F_c) in hertz is calculated as the product of relative cutoff frequency f_c and the signal frequency f. F_c was found to be 5.25 ± 0.9, 5.75 ± 0.8, 8.5 ± 1.5, 14 ± 1, and 16 ± 2 Hz at 1.25, 2.5, 5, 10, and 20 Hz, respectively. F_c, plotted in Figure 2B as a function of flicker frequency, was described by $F_c = mf^p$, where m and p are constants. The best fit of this equation to the data was obtained with $m = 4.88$ and $p = 0.42$.

DISCUSSION

When the duration of the noise frame increases, the spectral density below the high-frequency cutoff increases, whereas its cutoff frequency decreases in proportion to the frame's dura-

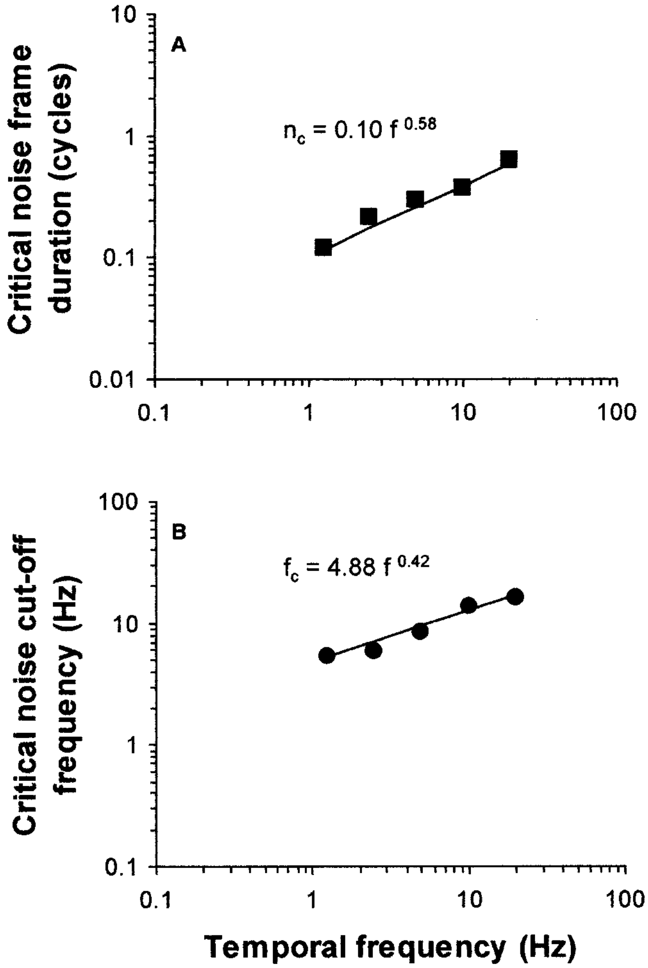

FIGURE 2. (A) Critical noise frame duration, corresponding to the longest duration still mimicking white noise, plotted as a function of flicker frequency. (B) Critical high-frequency cutoff of white noise in hertz plotted as a function of flicker frequency.

tion. For a range of short noise frame durations, only the former effect was evident as energy threshold for flicker detection increased in proportion to frame duration and kept the nominal *SNR* constant. This means that the masking effect of external, purely temporal noise increased with the duration of the noise frame, mimicking white noise, despite its decreasing bandwidth. For longer noise frame durations, temporal noise did not elevate the detection threshold enough to keep the nominal *SNR* constant, because the decreasing cutoff frequency began to curtail even those noise frequencies that interfered with detection. The white part of the noise spectrum thus no longer extended across the whole bandwidth used for detection. This is analogous to our previous results on spatial masking.[10,11]

At the cutoff frequency corresponding to the duration of the critical noise frame, the average power spectrum of noise was 41% of its maximum (see equation 2), and at higher frequencies it decreased further in an undulating fashion. When the cutoff frequency of the noise fell below the temporal frequency corresponding to the critical noise frame duration, the spectral density of noise averaged over the frequency range of the detector decreased below N_0. Hence, the zero-frequency spectral density given by equation 3 is no longer a valid measure of the effective noise. Noise has become nonwhite within the bandwidth of the detection filter.

The increase of the masking effect of external temporal noise with noise frame duration broadens the use of noise in experimental and clinical research. Both diseases of the visual system and the choice of signal parameters can produce poor sensitivity to temporal contrast, which implies that the contrast of external noise is also attenuated. Because high signal contrast is needed for threshold measurement, the remaining contrast range is not sufficient to produce external noise that is stronger than internal noise. If the spectral density of noise is increased by increasing the duration of the noise frame, however, noise contrast can be kept low, and more of the dynamic range of the display is left for the signal. The critical noise frame duration for the signal used must not be exceeded, however.

The critical duration expressed in terms of a fraction of a cycle increased with flicker frequency. The higher the frequency, the fewer noise frames were needed per cycle to mimic white noise. This differs from spatial vision, for which the critical noise check size expressed as a fraction of spatial cycle is constant, independent of the spatial frequency of the signal with constant bandwidth.[10,11]

In the chain of processes[1,2] determining flicker sensitivity, the source of the frequency dependence described herein may be the early physiological transformations shaping neural signals or/and the central signal detector. It would be easy to accommodate the results by ad hoc assumptions about the bandwidths of the matched filter or multiple channels. This is not, however, in agreement with the finding that temporal integration is independent of temporal frequency.[15,16] It is, therefore, more likely that the frequency dependence of critical duration originates from known physiological properties of peripheral processing that modify the neural signals before detection.

In a matched filter model, the detector is assumed to be a replica of the signal. If the bandwidth and center frequency of the neural signal at the level of detection were equal to the external signal, the critical number of noise frames per signal cycle should be constant for our signals with constant bandwidth. The results, however, show that detection of flicker at 1.25 Hz was affected by noise up to approximately 4.2 times the nominal signal frequency. The corresponding factors were approximately 2.3, 1.7, and 1.4 at 2.5, 5, and 10 Hz. This means that the lower the nominal center frequency, the more its bandwidth will spread toward higher temporal frequencies.

Considering the known retinal mechanisms, it seems plausible that the power spectrum of the neural signal could spread to frequencies significantly higher than the nominal signal frequency, especially at low flicker frequencies. There are good grounds for thinking that human achromatic flicker detection is based on signals in M-type retinal ganglion cells.[2,9,17] The nonlinear M_Y cells, such as cat Y cells, give both fundamental and frequency-doubled responses to temporal modulation. The relative amplitudes of these components depend on the parameters of stimulation,[18,19] but the frequency-doubled component is relatively favored by large-field stimuli that extend far into the receptive field surround, as in the present experiments. Moreover, linear responses at the fundamental frequency (whether in M_Y cells or in the larger population[20] of M_x cells) would be comparatively weak for large-field flicker at low frequencies.[21,22] Additional neural modulation above the nominal frequency could come from the convergence of inputs from ON-center and OFF-center cells. We do not know how the brain integrates inputs from different cells and cell types, but a simple assumption would be that detection occurs whenever any type of neural response exceeds a certain *SNR*. The relative weight of different response types will automatically vary with flicker frequency, and as signal frequencies approach the temporal high-frequency roll-off of the ganglion cell, higher harmonics will be particularly strongly attenuated, and the fundamental will become dominant. With respect to the nature of the neural signal, it is worth pointing out that the threshold percept of flicker without external noise is quite indeterminate and, specifically, does not correspond to the objective signal frequency.[23]

Retinal low-pass filtering can in principle shift the spectral peak of the neural response somewhat below the nominal frequency at high temporal frequencies. This would occur if the flicker frequency is on the falling high-frequency limb of the modulation transfer function (of an M-cell, for example) resulting in such severe filtering at and higher than 20 Hz that the amplitude of the signal (and noise) is relevant mainly at frequencies below the nominal frequency of the signal. In agreement with this, at 20 Hz the critical cutoff frequency of the noise appears to be slightly below the expected minimum value of two noise frames per flicker cycle (i.e., the cutoff frequency of noise equal to the flicker frequency).

Flicker detection has also been modeled[3,4] using a multiple channel approach in which detection is mediated by one broadly tuned low-pass channel and one broadly tuned band-pass channel that includes quite low frequencies but rolls off sharply at higher than 20 Hz. If any subset of our signals were detected using just one of these channels, the critical cutoff frequencies of these signals would correspond to the cutoff of the channel. This could be the case for our signals at 1.25 and 2.5 Hz, because their critical noise cutoff frequencies were almost the same (5.3 and 5.8 Hz) and roughly correspond to the cutoff of the broadly tuned low-pass channel.[4] The increase of critical noise cutoff frequency to 14 Hz when our signal frequency increased to 10 Hz could reflect a combination of the responses from the two channels.[4] Our 20-Hz signal could be detected using only the band-pass channel, because its peak response was at approximately 20 Hz, and at this frequency the response of the low-pass channel had dropped to one tenth of its maximum. The total amount of noise that affects detection should therefore start decreasing as soon as the noise cutoff frequency decreases below the cutoff frequency of the band-pass channel. The critical cutoff frequency of noise therefore should be above the nominal signal frequency, in disagreement with our experimental finding of 16 Hz.

We conclude that the masking effect of external, purely temporal noise can be increased by increasing the noise frame duration up to a critical value. However, the critical duration, in terms of a fraction of flicker cycle, increases with flicker frequency, in contrast to the situation in analogous experiments on spatial masking.[10,11]

References

1. Rovamo J, Raninen A, Lukkarinen S, Donner K. Flicker sensitivity as a function of spectral density of external white temporal noise. *Vision Res.* 1996;36:3767–3774.
2. Rovamo J, Raninen A, Donner K. The effects of temporal noise and retinal illuminance on foveal flicker sensitivity. *Vision Res.* 1999; 39:533–550.
3. Fredericksen RE, Hess RF. Temporal detection in human vision: dependence on stimulus energy. *J Opt Soc Am A.* 1997;14:2557–2569.
4. Fredericksen RE, Hess RF. Estimating multiple temporal mechanisms in human vision. *Vision Res.* 1998;38:1023–1040.
5. Ahumada AJ Jr, Watson AB. Equivalent-noise model for contrast detection and discrimination. *J Opt Soc Am A.* 1985;2:1133–1139.
6. Legge GE, Kersten D, Burgess A. Contrast discrimination in noise. *J Opt Soc Am A.* 1987;4:391–404.
7. Burgess AE, Wagner RF, Jennings RF, Barlow HB. Efficiency of human visual signal discrimination. *Science.* 1981;214:93–94.
8. Pelli D. Effects of visual noise. Thesis. Cambridge, UK: Cambridge University; 1981.
9. Rovamo J, Donner K, Näsänen R, Raninen A. Flicker sensitivity as a function of target area with and without temporal noise. *Vision Res.* 2000;40:3841–3851.
10. Kukkonen H, Rovamo J, Näsänen R. Masking potency and whiteness of noise at various noise check sizes. *Invest Ophthalmol Vis Sci.*1995;36:513–518.
11. Rovamo J, Kukkonen H. The effect of noise check size and shape on grating detectability. *Vision Res.* 1996;36:271–279.
12. Kukkonen H, Rovamo J, Melmoth D. Spatial integration and effective spectral density of one-dimensional noise masks. *Vision Res.* 1999;39:1775–1782.
13. Pelli DG, Zhang L. Accurate control of contrast on microcomputer displays. *Vision Res.* 1991;31:1337–1350.
14. Mustonen J, Rovamo J, Näsänen R. The effects of grating area and spatial frequency on contrast sensitivity as a function of light level. *Vision Res.* 1993;33:2065–2072.
15. Watson AB. Probability summation over time. *Vision Res.* 1979; 19:515–522.
16. Raninen A, Rovamo J. Modelling of flicker sensitivity as a function of exposure time [ARVO Abstract]. *Invest Ophthalmol Vis Sci.* 1995;36(4):S907. Abstract nr 4168.
17. Purpura K, Tranchina D, Kaplan E, Shapley RM. Light adaptation in the primate retina: analysis of changes in gain and dynamics of monkey retinal ganglion cells. *Vis Neurosci.* 1990;4:75–93.
18. Hochstein S., Shapley RM. Quantitative analysis of retinal ganglion cell classifications. *J Physiol.* 1976;262:237–264.
19. Hochstein S, Shapley RM. Linear and nonlinear spatial subunits in Y cat retinal ganglion cells. *J Physiol.* 1976;262:265–284.
20. Kaplan E, Shapley RM. X and Y cells in the lateral geniculate nucleus of macaque monkeys. *J Physiol.* 1982;330:125–143.
21. Frishman LJ, Freeman AW, Troy JB, Schweitzer-Tong DE, Enroth-Cugell C. Spatiotemporal frequency responses of cat retinal ganglion cells. *J Gen Physiol.* 1987;89:599–628.
22. Donner K, Hemilä S. Modelling the spatiotemporal modulation response of ganglion cells with difference-of-gaussians receptive fields: relation to photoreceptor response kinetics. *Vis Neurosci.* 1996;13:173–186.
23. Roufs JAJ. Dynamic properties of vision. I: experimental relationships between flicker and flash thresholds. *Vision Res.* 1972;12: 261–278.