# Preference of Sensory Neural Coding for $1/f$ Signals

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We investigated the influences of different types of temporal correlations in the input signal on the functions and coding properties of neurons in the primary visual cortex (V1). We found that the temporal transfer functions of V1 neurons exhibit higher gain, and the spike responses exhibit higher coding efficiency and information transmission rates, for the $1/f$ (natural long-term correlation) signals than for $1/f^0$ (no correlation) and $1/f^2$ (stronger long-term correlation) signals. These results suggest that the intermediate long-term correlation ubiquitous to natural signals may play an important role in shaping and optimizing the machinery of neurons in their adaptation to the natural environment.

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Sensory neurons have been found to encode natural signals more efficiently than artificial signals [1]. What are the statistical features inherent in natural signals contributing to this enhanced efficiency? It is well known that long-term correlation is a common feature in the second order statistics of natural signals [2]. In the frequency domain, temporal signals with natural long-term correlations generally exhibit a $1/f$-type power spectrum, while those with no correlation or stronger long-term correlations show $1/f^0$ or $1/f^2$ power spectra. The $1/f$ characteristic is ubiquitous in one-dimensional natural signals, such as the velocity of ocean waves [3], the loudness of natural sounds [4], the temporal luminance variation in natural scenes [5], and the spiking activities of cortical neurons in the brain [6]. Meanwhile, $1/f^0$ and $1/f^2$ characteristics are usually observed in artificial signals. Since mammalian visual systems have evolved in the natural environment, the statistical properties of signals in natural scenes may play an important role in shaping their structures and functions.

Recent studies indicate that appropriate correlations in the input signals can significantly affect the sensitivity of sensory neurons [7]. Correlated inputs to sensory neurons are found to induce irregular spiking responses with high spike timing precision and signal-to-noise ratios. Background noise with long-term correlation can also greatly facilitate the sensitivity of the neurons to subthreshold periodic signals [8]. Furthermore, proper long-range correlations have also been found to be important for efficiency in engineering systems, such as traffic control and neural models [9]. In this study we investigated whether the correlation in natural signals plays a role in neural adaptation and coding by studying the effects of different types of correlations on the response sensitivities and coding properties of sensory neurons. To simplify the study, we only examined the coding properties of neurons in the primary visual cortex (V1) for temporal signals, though the spatial statistical correlations of natural images may play a similar role in shaping the spatial coding properties of the neurons.

Single-unit recording techniques were used to record the spiking activities from 64 well isolated V1 neurons of two awake macaque monkeys, each presented with sine-wave gratings [Fig. 1(a)] featuring the designated $1/f^\beta$ temporal signals [10]. In each trial, the animals performed a fixation task on a dot at the center of the computer monitor for a liquid reward. The grating was shown in a 5 ° aperture centered on the receptive field (RF) of a cell being recorded. Eye position was monitored with an implanted ocular search coil, and trials were aborted if eye position deviated more than 0.5 ° from fixation. In each trial, the sinusoidal grating moved back and forward perpendicularly to the orientation of the grating [Fig. 1(a)] so that the temporal variation of the grating luminance varying with time obeyed a particular designated $1/f^\beta$ (where $\beta = 0$, 1, or 2) power spectrum [Fig. 1(b)]. The total power of the three classes of signals was equalized to avoid bias, i.e.,

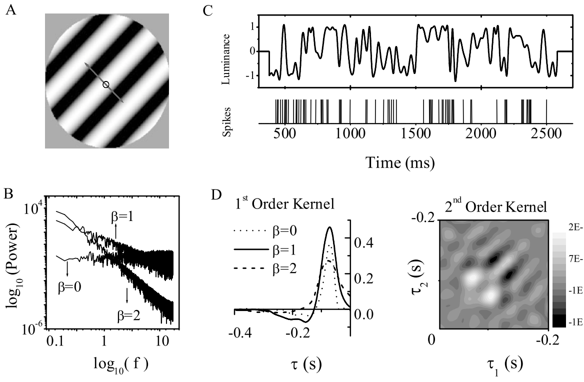

FIG. 1. (a) An example of a sine-wave grating. The line with arrows indicates the motion direction of the drifting grating. (b) The power spectra for the three classes of $1/f^\beta$ signals with $\beta = 0$, 1, 2, respectively. (c) An example of an input signal, specifically the time series of luminance intensity of the grating, and a sequence of resulting spike responses. (d) The first order kernels recovered from the three classes of signals (left) and the second order kernel recovered from the $1/f$ signals (right).

$\int_{f1}^{f2} P(1/f^0)df = \int_{f1}^{f2} P(1/f^1)df = \int_{f1}^{f2} P(1/f^2)df$, where $P(f)$ denotes the power spectrum of the signal, and $f_1$ (0.1 Hz) and $f_2$ (in the range of 18–27 Hz) are the low and high cutoff frequencies, respectively. A cutoff frequency is chosen so that all three classes of signals can drive the cells effectively with roughly the same mean firing rate. The orientation and spatial frequency of the grating were chosen according to the optimal spatial tuning of the recorded neuron. For each neuron, we presented three classes of $1/f^\beta$ signals with $\beta = 0$, 1, and 2, respectively. For each class of signals, 300 trials of random stimulus sequences and 60 repeated trials of a particular stimulus sequence were presented, with each trial lasting for 2.2 sec. Figure 1(c) gives an example of an input stimulus trial and a spike train of a neuron.

We first studied the effects of different types of temporal correlation in the signals on the performance functions of V1 neurons. Using 300 trials of random stimulus sequences and the output spike trains of each neuron, we recovered the temporal transfer function of the neuron in terms of the first (linear) and second order (quadratic nonlinear) Volterra kernels [11] [see Fig. 1(d) for an example], which capture the main property of the neuron and can be used to predict the neural response to any input signal used in this study. The first order kernel recovered from the $1/f$ type of signal has the highest amplitude gain compared to the kernels recovered from the other two types of signals. The peaks around $-80$ ms indicate that the neuron is preferentially sensitive to stimulus components occurring at around 80 ms prior to the spike. The second order kernel [see an example in Fig. 1(d)] depicts the finely correlated structures in the stimulus that induce a spike response. These observations suggest that these V1 neurons are sensitive to both the timing of the input signal and the temporal correlations among the different stimulus components in the signal.

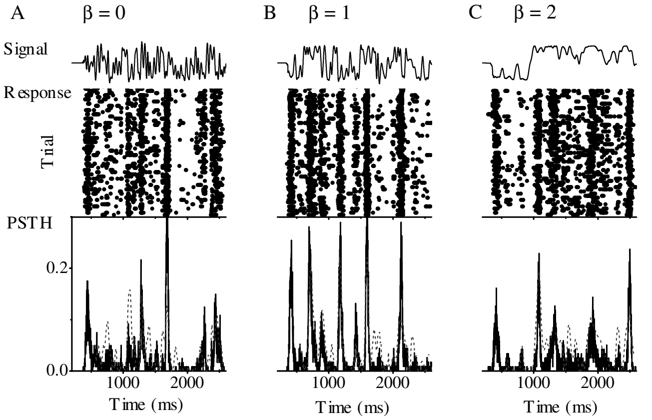

FIG. 2. Input signals with $\beta = 0$ (a), $\beta = 1$ (b), and $\beta = 2$ (c), and a V1 neuron's corresponding spiking responses in raster plot (middle) and PSTH (bottom). In the PSTH, the dotted lines represent the predicted responses and the solid lines represent the actual neural responses.

The temporal correlation structures in the signal may provide an additional driving force to excite the neuron in a stronger and a more precise manner. Figure 2 shows an example of a typical neuron's 60 repeated responses to the three types of input signals ($\beta = 0$, 1, 2). The neural responses as shown in the post-stimulus time histogram (PSTH) and raster plot for $1/f$ signals are stronger, more repeatable, and exhibit higher spike timing precision than that for $1/f^0$ and $1/f^2$ signals. The prediction of neural responses according to the first and second order kernels (plotted in the dotted lines) recovered using the $1/f$ signals are also more accurate than that using kernels recovered from the $1/f^0$ or the $1/f^2$ signals. To quantify the prediction accuracy precisely, we computed the Pearson's correlation coefficient between the actual response and the predicted response. Figure 3 shows that for almost 70% neurons, the kernels recovered from $1/f$ signals (i.e., $K_{\beta=1}$) can predict better than the kernels $K_{\beta=0}$ [Fig. 3(a)] and $K_{\beta=2}$ [Fig. 3(b)] according to the correlation coefficient (corr. coeff) measure. These results suggest that the coding function of the neuron may have been adapted to the long-term correlation in the natural signals so that the kernels recovered from the $1/f$ signals are closer to the real neural code. The signals with $\beta = 0$ or 2, meanwhile, may lack preferable components to the neurons, resulting in neural responses that reflect inadequately the underlying structures of the neural code.

To further verify the hypothesis that V1 neurons can encode $1/f$ signals better than the other types of signals, we introduce two information measures: coding efficiency and information transmission rate [12]. Coding efficiency is defined as $\varepsilon = I_\mathrm{m}/H(y)$, where $I_\mathrm{m}$ is the information in the response related to the stimulus (called "mutual information") and $H(y)$ is the total response entropy. The value $\varepsilon$ is used to quantify the fraction of a neuron's activity to encode the input signal. The information transmission rate, defined as $\gamma = I_\mathrm{m}/R$ ($R$ is the mean firing rate), quantifies how efficiently each individual spike carries information.

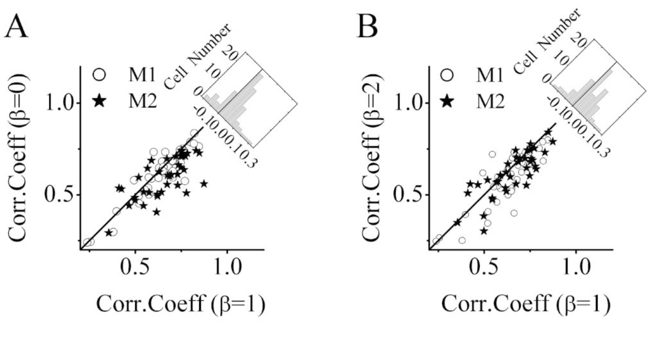

FIG. 3. (a) Population scatter plots of correlation coefficients for $K_{\beta=1}$ (i.e., corr. coeff $\beta = 1$) vs for $K_{\beta=0}$ (i.e., corr. coeff $\beta = 0$). Inset: the histogram for corr. coeff disparities. (b) Same comparison for $K_{\beta=1}$ vs $K_{\beta=2}$. M1 and M2 represent the two monkeys.

The direct method [13] is used to compute $I_{\mathrm{m}}$ and $H(y)$ from the spike trains.

Figures 4(a) and 4(b) compare the coding efficiency ($\varepsilon$) of the 64 V1 neurons to $1/f$ signals ($\beta = 1$) relative to $1/f^0$ ($\beta = 0$), and $1/f^2$ ($\beta = 2$) signals, respectively. The scatter plots show that, as a population, V1 neurons encode the $1/f$ signals with higher efficiency $\varepsilon$ than the $\beta = 0$ and $\beta = 2$ signals. The statistical analysis on the $\varepsilon$ disparity histogram demonstrates that the preference for $1/f$ signals is statistically significant [see insets of Fig. 4(a) and 4(b)]. Figures 4(c) and 4(d) show that the information transmission rate ($\gamma$) was also significantly higher for the $1/f$ signals as well. This means that each spike of the neuron can carry more information in the $1/f$ signal context than in the other types of signal contexts. The population mean of coding efficiency ($\langle\varepsilon\rangle$) is around 0.42 [Fig. 5(a)], and the population mean of information transmission rate ($\langle\gamma\rangle$) is around 1.6 bits/spike for $1/f$ signals [Fig. 5(b)]. These are comparable with other observed experimental results on neural coding of natural signals [1]. For the $1/f^0$ and $1/f^2$ signals, the mean coding efficiencies are significantly lower, at 0.38 and 0.3, respectively; the mean information transmission rates are around 1.42 and 1.28 bits/spike, respectively. These results provide strong evidence that the visual neurons can encode $1/f$ signals more efficiently than $1/f^0$ and $1/f^2$ signals.

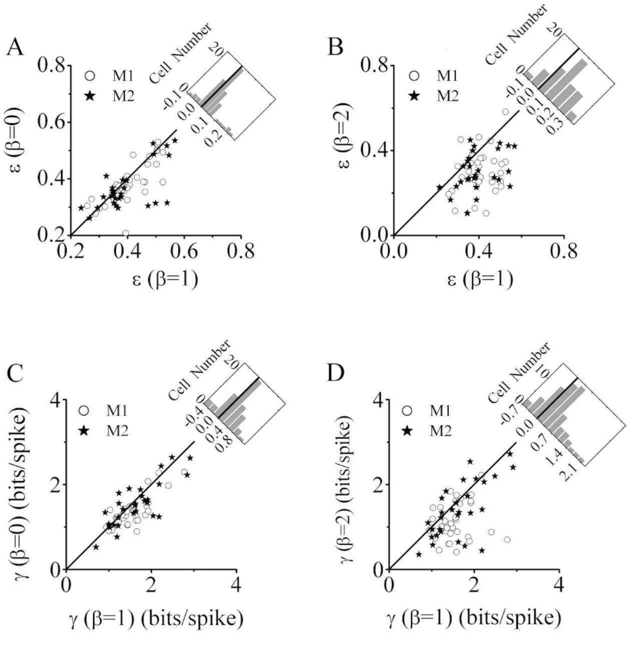

FIG. 4. (a) The coding efficiency $\varepsilon$ of the 64 neurons in response to the signals with $\beta = 1$ vs $\beta = 0$. (b) Similar comparison for $\beta = 1$ against $\beta = 2$. Inset: the histograms for coding efficiency disparity $\varepsilon(\beta = 1) - \varepsilon(\beta = 0)$ (a) and $\varepsilon(\beta = 1) - \varepsilon(\beta = 2)$ (b). (c) The information transmission rate $\gamma$ of the neurons for signals with $\beta = 1$ vs $\beta = 0$. (d) Same comparison for $\beta = 1$ against $\beta = 2$. Inset: the histograms for information transmission rate disparity $\gamma(\beta = 1) - \gamma(\beta = 0)$ (c) and $\gamma(\beta = 1) - \gamma(\beta = 2)$ (d).

The different classes of $1/f^{\beta}$ signals are characterized by different mean temporal frequencies (12, 8, 3 cycles/ sec). Could the better performance be a result of the temporal frequency tuning of the cells? Classically, the frequency tuning of the cells is determined by the average firing rates of the neurons to signals of different frequencies. Figure 5(c) shows that the mean firing rate $\langle R\rangle$ for $1/f^0$ signals was higher than that for $1/f$ and $1/f^2$ signals. Nevertheless, the coding performance of neurons for $1/f^0$ signals, however, was lower than for $1/f$ signals, as shown in Fig. 4. Therefore, the better coding performance of V1 neurons in the $1/f$ context is not purely a consequence of the tuning properties as measured by firing rates. This can be seen clearly in Fig. 5(d), which shows that the differences in coding efficiency for the three classes of signals ($\varepsilon_{\beta=1} - \varepsilon_{\beta=0}$ and $\varepsilon_{\beta=1} - \varepsilon_{\beta=2}$) are uncorrelated with the differences in firing rates $\Delta R$ (correlation coefficient $<0.001$). Although the differences in the information transmission rates ($\Delta\gamma$) are inversely proportional to $\Delta R$ [Fig. 5(e)], the mean $\gamma$ is always higher for the $1/f$ signals than for the other signals at each firing rate $R$ [Fig. 5(f)]. These results suggest that the temporal correlation inherent in a signal's energy distribution, rather than the mean temporal frequency, is a key feature in the stimulus responsible for the higher efficiency in neuronal coding.

While recent theoretical and experimental studies have showed that $1/f$ background noise could enhance the sensitivity of neurons to subthreshold signals better than white noise [8], ours is the first to demonstrate experimen-

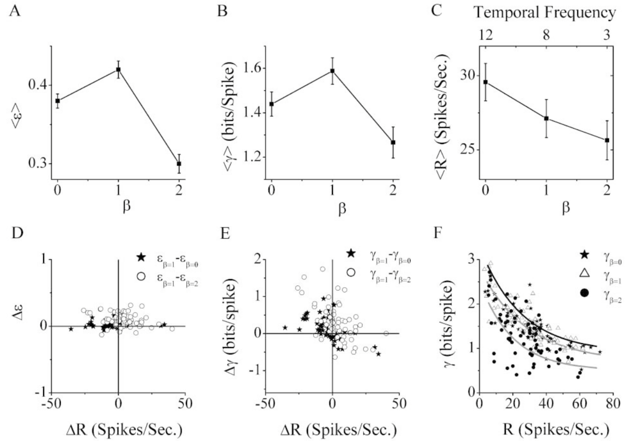

FIG. 5. The population means of coding efficiency $\langle\varepsilon\rangle$ (a), information transmission rate $\langle\gamma\rangle$ (b), and the spiking rate $\langle R\rangle$ (c) for the three classes of signals. Population scatter plots of $\Delta\varepsilon$ vs $\Delta R$ (d) and $\Delta\gamma$ vs $\Delta R$ (e). (f) Population scatter plot of $\gamma$ for the three classes of signals as a function of $R$; the colored lines are the exponential curves fitted by regression. Fitting functions are $0.8 + 1.7e^{-(x-4.5)/24}$ for $\beta = 0$, $0.9 + 2e^{-(x-4.5)/25}$ for $\beta = 1$, and $0.5 + 1.6e^{-(x-4.5)/20}$ for $\beta = 2$, respectively.

tally that the $1/f$ signals themselves can be encoded and transmitted by sensory neurons with higher efficiency. The power distribution of the $1/f^0$ and $1/f^2$ signals is dominant at high frequencies and low frequencies, respectively, while the $1/f$ signal power is the same in each frequency decade throughout the whole frequency range. Thus, the $1/f^0$ and $1/f^2$ signals might not be able to stimulate the V1 neurons fully, resulting in lower coding efficiency and information transmission rate. The fractal structures of natural signals generate many self-similar, irregular, and complex fluctuations at multiple time scales, resulting in the specific long-term correlations that are ubiquitous in natural signals. These fine correlational fluctuations likely modulate neural plasticity during evolution and development, resulting in higher coding efficiency and information transmission rates of neurons when exposed to natural signals. While other statistical features like phase or higher order statistics in natural signals might also influence neuronal coding, our results provide evidence that the $1/f$ characteristic may be a key feature in natural signals that the neurons adapt to, resulting in many of the recent experimental observations on efficient coding of natural signals in neural systems [1,14].

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[14] Recently, Jan W. H. Schnupp, Jose A. Garcia-Lazaro, A. J. King, and B. Ahmed at Oxford University, inspired by our study, found that neurons in the auditory cortex also exhibited tuning to $1/f$ signals (unpublished results).