Effects of phase correlations in naturalistic stimuli on quantitative information coding by fly photoreceptors

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Abstract

Natural visual scenes are rarely random. Instead, intensity and wavelength change slowly in time and space over many regions of the scene, so that neighboring temporal and spatial visual inputs are more correlated, and contain less information than truly random signals. It has been suggested that sensory optimization to match these higher order correlations (HOC) occurs at the earliest visual stages, and that photoreceptors can process temporal natural signals more efficiently than random signals. We tested this early stage hypothesis by comparing the information content of *Calliphora vicina* photoreceptor responses to naturalistic inputs before and after removing HOC by randomizing phase. Forty different, 60-s long, naturalistic sequences (NS) were used, together with randomized-phase versions of the same sequences to give pink noise (PN) so that each input pair had identical means, variances, mean contrasts and power spectra. We measured the information content of inputs and membrane potential responses by three different methods: coherence, mutual information, and compression entropy. We also used entropy and phase statistics of each pair as measures of HOC. Responses to randomized signals generally had higher gain, signal-to-noise ratio, and information rates than responses to NS. Information rate increased with a strong, positive, linear correlation to phase randomization within sequence pairs. This was confirmed by varying the degree of phase randomization. Our data indicate that individual photoreceptors encode input information by Weber’s law, with HOC within natural sequences reducing information transfer by decreasing the number of local contrast events that exceed the noise-imposed threshold.

New & Noteworthy

Natural visual scenes feature statistical regularities, or higher order correlations (HOC), both in time and space, to encode surfaces, textures, and object boundaries. Visual systems rely on this information; however, it remains controversial whether individual photoreceptors can discriminate and enhance information encoded in HOC. Here we show that the more HOC the stimulus contains, the lower the information transfer rate of photoreceptors. We explain our findings by applying the Weber’s paradigm of differential signal perception.
Introduction

It has been widely argued that visual systems are particularly effective in dealing with information encoded in natural scenes due to the unique statistical properties of the associated visual signals (Simoncelli 2003; Song and Juusola 2014; Rikhye and Sur 2015). At the individual photoreceptor level, the input consists of light intensity varying in time, while the response is a changing membrane potential. Unlike random noise inputs, natural signals can change slowly, giving a predominance of low-frequency components in their amplitude spectra of time-intensity series. The amplitude spectra of natural time-intensity series usually vary as $1/f^{0.5}$, where $f$ is the temporal frequency (van Hateren 1997), while amplitude spectra of natural images vary as $1/f_s$, where $f_s$ is the spatial frequency (Tolhurst et al. 1992). Due to the self-similar spatial organization, the $1/f_s$-type amplitude spectra (and, respectively, $1/f_s^2$ power spectra) reflect the spatial scales and objects in natural scenes over a wide range of depths or magnifications, regardless of whether the observer zooms in or out (Ruderman and Bialek 1994).

Temporal regularities in natural inputs to photoreceptors arise from the presence of intensity gradients representing surfaces, textures, and object boundaries in natural images, creating a high probability that the intensity sampled by a photoreceptor will be similar to recent intensities, rather than completely unrelated, as it would be in images or temporal sequences lacking such correlations. Statistically, such correlations are known as phase or higher order correlations (HOC). Their importance for visual perception was rigorously investigated during the last two decades in a number of studies of both vertebrates and invertebrates (Froudarakis et al. 2014; Song and Juusola 2014; Rikhye and Sur 2015; Friederich et al. 2016). It has been suggested that information encoded in HOC is more important for perception than the information contained in the signal amplitude/power spectra (Oppenheim and Lim 1981; Kovesi 2003; Hyvärinen et al. 2009).

Other important statistical characteristics of natural stimuli are high mean contrast, non-uniform and positively skewed stimulus amplitude distributions, and redundancy (Ruderman and Bialek 1994; van der Schaaf and van Hateren 1996; Hyvärinen et al. 2009). The first property is linked to the empirical observation that although natural stimuli are highly heterogeneous and variable, their mean amplitudes are usually relatively low (van der Schaaf and van Hateren 1996). These comparatively dark intervals in natural stimuli were suggested to be essential for high-capacity information transfer in fly photoreceptors (Song and Juusola 2014). The redundancy in natural stimuli results from the phase correlations described above. It can be measured by comparing the compression entropy of a stimulus before and after randomizing phase (Hyvärinen et al., 2009; French and Pfeiffer, 2011).
All the time-dependent features of natural visual scenes apply equally to the light intensity signals impinging on vertebrate or invertebrate eyes, but experimental advantages have caused photoreceptors of insect compound eyes to be important models of natural stimulus processing at the retinal level (Clark et al. 2013; Juusola and Song 2017). The low-pass filtering seen in the voltage responses of most insect photoreceptors fits remarkably well with the 1/f spectral structure of natural visual signals, allowing transfer of information encoded in the lower-frequency part of the power spectrum with minimal attenuation.

It remains unclear if or how HOC can affect signal processing in individual photoreceptors. Although it was suggested that fly photoreceptors reliably transfer information about local phase congruencies while suppressing random phase signals (Friederich et al. 2016), and that information sampling is more efficient for natural/naturalistic stimulation (Song and Juusola 2014), the question of whether the processing of HOC begins at the level of photoreceptors or whether photoreceptors simply encode intensity changes regardless of their phase structure remains unresolved. Simply put, can photoreceptors extract a larger proportion of the input information from natural versus random light intensity changes? Or, in other words, would the information rate in response to a stimulus with highly ordered phase exceed the information rate in response to a carefully matched random-phase stimulus, and what would be the cause of the difference?

To address this question, we performed a systematic investigation of the influence of HOC on information transfer in blowfly photoreceptors, using three different methods of estimating the information rate (IR). We compared photoreceptor responses to various naturalistic (NS) and matched randomized-phase stimuli (“pink noise”, PN), which were identical to NS but lacked HOC. Our findings indicate that, contrary to some earlier studies, individual fly photoreceptors process information encoded in visual stimuli without any particular regard for phase correlations, and that differences in response information rates evoked by different stimuli can simply be explained by the number of reliably detectable photon events contained in the stimulus.

**Materials and Methods**

**Experimental Design**

Young (2-6 days post eclosion) female blowflies were used in all experiments. Preparation and intracellular recordings were performed from broadband photoreceptors as described previously (Juusola et al. 1994; Takalo et al. 2011). In brief, alumosilicate microelectrodes (Harvard apparatus, UK) were manufactured using a laser puller (P-2000; Sutter Instruments, USA) and filled with 2 M potassium acetate solution; microelectrodes had resistances in the range of 100-130 MΩ. All recordings were amplified with an intracellular amplifier SEC-05L (NPI, Germany) and recorded at a sampling frequency of 2.4 kHz (DAQ-
board: PCIe-6259, National Instruments, USA; custom Matlab (Math-Works, Massachusetts, USA) software).

Photoreceptors were stimulated using a high-intensity green LED with a peak wavelength of 525 nm. Light stimulus was aligned with the photoreceptor’s optical axis. LEDs were calibrated using UV-Vis spectrometer USB4000 (Ocean Optics Inc., FL, USA). In the range of light intensities used for stimulation, dependence of LED light output on driving current was linear. Light intensity was attenuated using a series of neutral density filters (light levels ND0 to ND3 correspond to log(I/I₀) from 1 to -3). Experiments were performed at room temperature 20-22°C. All cells used for analysis had resting potentials of < -55 mV and responded robustly to light.

In our experiments, two types of recordings were performed. For thirteen out of forty stimulus pairs (see Results), responses were obtained at four light intensities. The recordings were conducted continuously from the lowest to the highest light level. The dark interval between recordings was ca. 15-30 s. The rest of data was obtained at the brightest level ND0, with the same 15-30 s intervals between recordings. While the recordings of the first type showed signs of light adaptation (Fig. 3A, B), responses of the second type usually did not (Fig. 7A, B). Because light adaptation during responses to non-saturating stimuli mainly affects initial voltage gain (French et al. 2016) and not information rate, and similarly modulates responses to both stimuli in the pair, we did not further control for light adaptation.

**Light stimuli**

Forty 60-s natural contrast sequences with dissimilar statistical properties were selected from van Hateren’s natural stimulus database (van Hateren 1997) (Fig. 1, black traces, presentation frequency of 1.2 kHz). For each stimulus, a surrogate “pink noise” (PN) sequence was created using the random phases algorithm (Theiler et al. 1992) (Fig. 1, grey traces). Each original natural sequence was Fourier transformed and then the phase values of each Fourier component were randomized. Finally, a new intensity time series was obtained by inverse Fourier transformation. Phase randomization usually yielded intensity values outside the initial NS range, including negative values, which could not be converted to light stimuli. To ensure that the original natural and the surrogate PN sequences had the same mean amplitude and mean contrast values (defined as standard deviation of the entire 60-s stimulus divided by its mean), the minimum (negative) value of the new PN sequence was subtracted from both stimuli. The stimuli were then scaled up by multiplying with the same factor so that one of them (usually the original stimulus) had a maximal value of 10, corresponding to the upper boundary of the light source voltage converter. Throughout the text, the modified natural sequences are therefore referred to as “naturalistic stimuli” or NS.
We note that no information was added or lost during the Fourier transformations, and the original NS could be precisely restored from its amplitude and phase spectra. However, the random phases meant that each inverse Fourier transformation resulted in a PN signal with the same second-order statistical properties but different temporal sequence. In other words, for every unique NS a large number of spectrally-matched surrogate PN stimuli could be produced. However, we only used one of all possible matching PN stimuli to each NS (Fig. 1).

To generate artificial signals with partially randomized phase, the phase spectrum of the original natural sequence obtained with Fourier transformation in the range from 0.0083 to 600.0000 Hz was altered in the following way. To obtain a stimulus with 25% of phase randomized, the phase was randomized within 1-Hz frequency intervals starting with 1, 5, 9 … 597 Hz. In other words, in the spectral interval spanning from 4 to 8 Hz, frequencies from 4 to 5 Hz and from 6 to 8 Hz had unaltered phase, while the frequencies between 5 and 6 Hz had random phase. To generate a stimulus with a 75% random phase, only the 1-Hz frequency intervals starting with 0, 4, 8 … 596 Hz retained their original phase.

**Data analysis**

Information content of each signal was evaluated by three different methods based on coherence ($H$) and two different estimates of signal entropy ($R$ and $E$).

The coherence information rate $H$ was estimated as described previously (Ignatova et al. 2014) using the coherence function, $\tilde{\gamma}^2(f)$:

$$\tilde{\gamma}^2(f) = \frac{|\hat{P}_{xy}(f)|^2}{\hat{P}_{xx}(f)\hat{P}_{yy}(f)}$$

where $\hat{P}_{xx}$ and $\hat{P}_{yy}$ are the stimulus and response power spectral density estimates and $\hat{P}_{xy}$ is their cross power spectral density estimate (Bendat and Piersol 2012). The estimates were obtained using Welch’s method with a 0.5-s Hanning window (1200 points resulting from 2.4 kHz sampling rate), and with a 50% overlap; FFT size was 2048. The coherence rate was estimated using the equation

$$H = - \int \log_2(1 - \tilde{\gamma}^2(f))df$$

in the frequency range from 1.2 Hz to 200.0 Hz (Stein et al. 1972; van Hateren and Snippe 2001). The coherence rate is an approximation of the information rate, when assumptions about the system’s linearity and Gaussian properties of inputs are not met. The coherence rate can be considered as a biased information rate; it is equal to Shannon’s information rate in the case of independent Gaussian signals and noise (van Hateren and Snippe 2001).

Mutual information ($MI$) can be defined as $MI = H(X) + H(Y) - H(X, Y)$, where $H(X)$ and $H(Y)$ are the entropies of the input and output, respectively, and $H(X,Y)$ is the joint entropy of $X$ and $Y$. Mutual
information rate $R$ was calculated from the equation $MI = R \cdot d + c$, where $d$ is the dimension of the random process and $c$ is a constant depending on the initial condition (Takalo et al. 2011). $R$ was estimated in nats/sample units as the linear slope of $MI$ function of a dimension $d$ and then this measure was divided by the sample interval and by log2 to yield bits/s units. The number of principal component analysis components used in MI estimates was set to 2 and the count of nearest neighbors to 5 (Takalo et al. 2011). Data were down-sampled to 600 Hz. This method requires only that the signal is stationary and ergodic. While PN stimuli satisfy these criteria, NS stimuli in general are not ergodic, although the method was originally tested using photoreceptors responses to three different NS (Takalo et al. 2011).

Compression entropy rates were calculated using the lossless data compression algorithm (French and Pfeiffer 2011). In brief, the signal is first represented as a series of alphanumeric symbols; next, it is compressed by iteratively replacing pairs of symbols that appear with the highest frequency by new symbols, until no further compression is possible. This approach calculates the minimum entropy required to reproduce the original signal from the compressed sequence. The compression entropy rate $E$ was calculated as $E = (N \cdot \log_2 M)/n \cdot t$, where $N$ is the number of symbols after compression, $M$ is the number of different symbols used, $n$ is the digitization level, and $t$ is the signal duration in seconds. A digitization level of 10 allowing 1024 amplitude levels was used as in the previous study (French and Pfeiffer 2011). $E$ values were calculated using custom software at a sample rate of 600 Hz.

It should be noted that, in contrast to entropy, the measurements of signal information based on coherence function ($H$) (van Hateren and Snippe 2001; Bendat and Piersol 2012), and probability densities ($R$) (Takalo et al., 2011) discard phase information and therefore do not measure temporal redundancy.

Photoreceptors generate bump noise due to photon arrival, which decreases with light adaptation and depolarization (Wu and Pak 1978; Lillywhite and Laughlin 1979; Frolov et al. 2017). This can be seen in the entropy rate trends of Fig. 3H and in the negative correlations between stimulus mean amplitude and entropy rates for NS and PN responses at ND0 (Table 4). The compression entropy algorithm interprets this noise as additional entropy. Several approaches can be used to minimize this error, including averaging repeated responses (Pfeiffer and French 2009) or calculation of noise entropy from appropriate responses to steady light pulses followed by correction of the original rates. However, confusion of bump noise with transduced information was not an issue here because we measured differences between entropy values for each stimulus pair, rather than the absolute values. Because NS and PN stimuli in each pair produced voltage responses with similar average sustained depolarization amplitudes (see Discussion), the associated noise entropies were expected to be approximately equal, and to cancel out from entropy differences.

**Statistical Analyses**
All values are presented as mean ± s.d.; in figures, error bars designate standard deviation. Pearson’s correlation coefficient (r) and Spearman’s rank order correlation coefficient (SROCC, ρ) were used in the analysis of correlations as indicated. Correlations were considered to be significantly different from zero when P < 0.05. Paired Student’s t-test was used for data comparison as indicated. Throughout the text (n) indicates sample size.

Results

The experiments and analysis presented below are divided into five parts. (1) The input stimuli and their important statistical properties (Figs. 1 and 2, Tables 1 and 2). (2) General results of photoreceptor stimulation with forty stimulus pairs (Figs. 3 and 4, Tables 3 and 4). (3) Partial phase randomization experiments (Fig. 5), to validate the conclusions of Part 2 experiments. (4) How background intensity affects information processing (Figs. 6 and 7). (5) A mechanistic explanation for the findings (Fig. 8).

1. Input stimuli and their statistical properties

To determine how HOC present in natural scenes affect information processing at the level of individual photoreceptors, we analyzed and compared photoreceptor responses to a pair(s) of stimuli, one of which was natural, or had the most important aspects of natural sequence statistics, whereas the other was identical, except for lacking the phase correlations. As the Fourier amplitude (or power) spectrum depicts second-order correlations between pixels in a spatial series or between light intensities in a temporal series, the phase spectrum reflects HOC, encoding information about such features as gradients, boundaries and changes of contrast, including their exact location in the sequence. Therefore, by randomizing the phase spectrum of a natural sequence, it is possible to abolish HOC while keeping the original amplitude spectrum intact. We used this approach to generate surrogate matches for forty 60-s natural sequences with dissimilar statistical properties. Examples of these new “naturalistic” and matched “pink noise” stimuli are shown in Figure 1. For three stimulus pairs (NS/PN#1, 24, and 34) the stimuli are also shown as single-pixel image arrays. In addition to the nearly zero phase spectra, PN stimuli were characterized by Gaussian amplitude distributions, whereas NS had irregular amplitude distributions.

The amplitude and phase spectra are shown in Figures 2A and B. The amplitude spectra were identical for NS and PN within each pair but differed widely between the pairs (Fig. 2A). Phase spectra were variable for NS but not for PN stimuli (Fig. 2B). Upwardly trending phase spectra found in 13 of 40 NS indicate that higher frequency components in these sequences generally precede lower frequency components.

The redundancy associated with natural stimuli can be measured from compression entropy because compression is more efficient with a predictable sequence (Hyvärinen et al. 2009). When changes in entropy
were measured for 60-s stimuli with 1-s sampling rate, it was found that feature-rich aspects of naturalistic stimuli are associated with peaks in entropy, $E$, whereas fluctuations in $E$ were relatively small for PN (Fig. 2C). In all the following experiments we used $E$ rates for the entire 60-s stimuli. Entropy rates for all input stimuli are shown in Figure 2D. In this and all other figures the stimuli are arranged in the order of decreasing entropy rate differential within each pair so that NS/PN#1 pair is characterized by the largest \( \Delta E = E_{PN} - E_{NS} \) value, and NS/PN#40 – by the smallest. The stimuli shown in Figure 1 are numbered and presented in the same way.

All PN stimuli had very similar entropy rates, $580 \pm 7$ bits s$^{-1}$ on average, despite displaying prominent differences in both amplitude distributions (Fig. 1) and amplitude spectra (Fig. 2A). We correlated the differences in absolute phase values at 200 Hz and $\Delta E$ values for each stimulus pair (henceforth referred to as phase and entropy differentials, respectively) and found a strong positive correlation ($\rho = 0.79, P < 10^{-5}$, Fig. 2E) suggesting that both entropy and phase can be used as proxies for the level of HOC in the naturalistic sequences. Table 1 lists main statistical properties of the stimuli.

The relationship between entropy and HOC is straightforward because the ordering effect of HOC on neighboring points in the intensity time series directly reduces entropy. The relationship to phase differences may be less intuitive because it reflects exactly the same ordering effects, but in the frequency domain.

2. Responses of fly photoreceptors

Typical responses of a blowfly photoreceptor to NS/PN#3 stimulus pair at four light intensities are shown in Figure 3A, B. Power spectra of inputs and responses for the highest stimulus intensity (ND0) are shown in Figure 3C. Despite the identical input power spectra, the voltage response to NS#3 (blue traces in Fig. 3A and C) was characterized by lower power in the low-frequency region than the response to PN#3 (blue trace in Fig. 3B, white triangle trace in Fig. 3C). This difference was also reflected in the gain (output/input as a function of frequency) and signal-to-noise ratio (SNR) functions (Fig. 3D, E). Three methods were used to quantify the transfer of information from input light intensity to output membrane potential changes: the coherence-based measure ($H$), the mutual information rate ($R$) based on principal component analysis of probability distributions, and the compression entropy ($E$) based on minimum symbolic representation (see Methods). Although the applicability of all three methods to analysis of photoreceptor responses elicited by non-linear and non-ergodic stimuli is limited, they yielded a consistent result: information transfer rates were higher for responses to PN than to NS.

Dependencies of $H$, $R$, and $E$ rates on membrane depolarization for the entire experimental group of five photoreceptors are shown in Figure 3F-H, respectively. Values of $H$ and $R$ generally increased with
light intensity and depolarization, whereas compression entropy rates decreased (Fig. 3F-H). Nevertheless, photoreceptor responses to PN#3 had consistently higher $E$ values than responses to NS#3. Decrease in entropy rate with increased membrane depolarization is typical for light responses of insect photoreceptors because the voltage response contains a large quantum bump (photon) noise component that is interpreted as entropy, but decreases with illumination and depolarization of the photoreceptor (See Methods and also section 4 of Results).

Mean IRs calculated separately for different background intensities are shown in Figures 3I-K. At the lowest light level, ND3, both $H$ and $R$ rates were small, with small differences between NS and PN. However, the differences increased with light intensity, with the largest differences found for the coherence-based method at two brightest intensities, ND1 and ND0 (Fig. 3I). For instance, at ND0, the $H$ rates were $138 \pm 12$ and $239 \pm 27$ bits s$^{-1}$ for NS#3 and PN#3, respectively ($P < 0.001$, $t$-test), the $R$ rates were $62 \pm 1$ and $70 \pm 3$ bits s$^{-1}$ for NS#3 and PN#3, respectively ($P < 0.001$, $t$-test), and $E$ rates were $414 \pm 18$ and $460 \pm 11$ bits s$^{-1}$ for NS#3 and PN#3, respectively ($P = 0.0012$, $t$-test).

This pattern, of the largest output IR differentials obtained using the coherence-based method, was found consistently throughout this study (Fig. 4). The same approach, involving recordings at four background intensities, was used for 13 NS/PN pairs. After it was established that the largest differences between NS and PN were registered in the brightest light and that there was no saturation, further recordings were performed at the brightest ND0 intensity only, to streamline data acquisition.

Actual average rates $H$, $R$, and $E$, at ND0 for all forty pairs of stimuli are shown in Table 3. When input phase $\Delta \Phi = \Phi_{PN} - \Phi_{NS}$ and input entropy $\Delta E = E_{PN} - E_{NS}$ differentials were correlated to the normalized output IR differences $(H_{PN} - H_{NS})/H_{PN}$, $(R_{PN} - R_{NS})/R_{PN}$, and $(E_{PN} - E_{NS})/E_{PN}$ strong positive correlations emerged in all cases (Fig. 4A-F, Table 4). Assuming that all three methods provide imprecise approximations for the output IR, we combined their scores by averaging the three normalized output IR differences $((H_{PN} - H_{NS})/H_{PN}$, $(R_{PN} - R_{NS})/R_{PN}$, and $(E_{PN} - E_{NS})/E_{PN})$. Correlations between input phase/entropy differentials and the averaged normalized IR differences were stronger (Fig. 4G: $\rho = 0.78$, $P < 0.001$; Fig. 4H: $\rho = 0.91$, $P < 10^{-5}$) than the correlations of individual output IR measures (Fig. 4A-F).

3. Partial phase randomization

The above results suggested that information content in natural sequences decreases progressively with increasing amount of HOC. However, direct comparison between sequences with different statistical properties would be unreliable. Therefore, we studied how increasing phase randomization of the same NS would affect information transfer. In these experiments any influences of mean contrast, mean amplitude, and variance between inputs would be eliminated.
We created two stimuli with a partly randomized phase, of 25% and 75%, using NS#3 and compared the responses they elicited (Fig. 5A, B). All four sequences had identical power spectra, mean amplitudes and mean contrasts. A sequence with 50% randomized phase was not used because it contained prominent negative transients, which required large baseline elevation for all stimuli, resulting in a decreased mean contrast. The phase spectra and entropies of all four inputs are shown in Figures 5B and C. Responses from two photoreceptors showed that the stimuli with partly randomized phases elicited responses with IR values between the original NS#3 and PN#3 (Fig. 5D-F), as predicted.

4. Effects of background intensity

While the naturalistic sequences used in the forty stimulus pairs retained their original spectral properties, their mean amplitudes had to be increased by varying amounts to remove negative values in the generated PN sequences (see Methods). This led to two important effects: NS had comparatively low mean contrast and lacked fully dark intervals. However, these are both prominent features of natural sequences and might significantly affect the transfer of information by photoreceptors. Specifically, it was previously suggested that the ubiquitous presence of dark intervals facilitates the recovery of microvilli from inactivation and assists in encoding important environmental cues (Song and Juusola 2014; Juusola and Song 2017). Therefore, we tested how (1) manipulation of NS baseline can affect information transfer, and (2) how differences in IRs within stimuli pairs are affected by mean intensity level.

In the first experiment, the effects of elevated baseline were tested using the natural sequence of NS#31 (Fig. 6) which had high variance (Table 1) and contained comparatively little HOC. As expected, the stimulus with the lowest baseline and mean intensity elicited a response with the highest gain (blue traces, Fig. 6A, B). However, the IRs measured with different methods were similar for all three backgrounds (averages from three photoreceptors are shown). Only a slight decrease can be seen for the stimulus with the background intensity of 3.46 and the relatively low mean contrast of 0.33 (Fig. 6E). These experiments suggest that the presence of dark intervals does not improve information processing, probably because improved signal resolution due to increased gain is offset by increased bump (photon) noise, which reduces coherence and SNR in the low frequency region (Fig. 6B-D).

However, since HOC were not prominent in NS#31, we also used stimulus pair #3 to evaluate effects of baseline increase on the NS/PN IR differential (Fig. 7). No matching PN stimulus could be constructed for the NS with the lowest mean intensity (0.04, blue traces in Fig. 7A-E, first points in Fig. 7F-H). At higher mean intensity levels, five NS/PN stimulus pairs were used; notice that Figure 7A illustrates only two such pairs with the corresponding typical responses (mean amplitudes of 0.24 and 1.04, green/pink and black/red traces). Importantly, IR values calculated using the methods sensitive to noise –
coherence and mutual information - indicated a sharp deterioration in information transfer with increased mean stimulus amplitude (Fig. 7F, G).

The situation for normalized output IR differences between NS and PN was more complex. When averaged normalized IR differences were plotted against mean stimulus amplitude, it was found that they decreased strongly with increasing mean amplitudes (Fig. 7I). Considering that the stimulus pairs used in this study were characterized by different mean amplitudes (Table 1), this finding raised a question whether the decrease in the IR differences reported above (Fig. 4) could be partly caused by higher mean amplitudes of the inputs, which also correlated strongly negatively with our measures for HOC (Table 2). Indeed, the averaged IR differences correlated strongly negatively with the mean amplitudes of the stimuli ($\rho = -0.76$, $P < 10^{-6}$, Table 4).

While this correlation may appear to support a crucial role of mean amplitudes in determining the IR differences between NS and PN, other data are not consistent with it. Firstly, $H$ and $R$ information rates did not consistently decrease with increasing mean amplitudes (Table 4). (Although significant negative correlations were found between mean stimulus amplitude and $E$ values for NS ($\rho = -0.64$, $P < 10^{-5}$, Table 4), and between mean stimulus amplitude and $H$ and $E$ values for PN (respectively $\rho = -0.65$, $P < 10^{-5}$, and $\rho = -0.91$, $P < 10^{-5}$, Table 4), the decreases in $E$ were caused by reduction in bump noise and noise entropy due to increasing stimulus intensity.)

It is more likely that mean amplitude affects IRs indirectly, via mean contrast (mean contrast = standard deviation/mean amplitude). A clear negative correlation can be seen between mean contrast (values in Fig. 7G) and IRs and averaged IR differences in Figure 7F, G, I. These findings are explained below using the concept of physiological limitation of signal detection. However, since mean contrast varied little in the main sample (from 0.21 to 0.34, Table 1), and no correlation was found between mean contrast and output IRs for $H$ and $R$ (Table 4), the background-related findings are largely irrelevant to the conclusions drawn from the main experimental group.

5. HOC, local contrast, and output information rates

How can the presence of HOC reduce the photoreceptor IR? We propose that this is a consequence of the intrinsic physiological limitations of photoreceptors in perceiving signals with small temporal gradients that are associated with HOC in natural visual signals. Like any other biological receptor system, the threshold of visual system resolution is governed by Weber's law; specifically, by the concept of just noticeable difference, or Weber's constant, incorporated therein, which states that for a change in brightness to be detectable, the change $\Delta I = I_{n+1} - I_n$, where $I_n$ is the previous and $I_{n+1}$ the next value of stimulus intensity, should exceed a certain dynamic threshold, $|\Delta I_{\text{min}}|$, that defines a small but constant proportion $|\Delta I_{\text{min}}|/I_n =...
In other words, the larger the previous value, the larger the change in intensity must be for perception, and \textit{vice versa}.

Figure 8A demonstrates distributions of \textit{local contrasts} in four stimuli used in partial phase randomization experiments (Fig. 5A). Local contrast is defined here as \((I_{n+1} - I_n)/I_n\). To account for the time constant due to capacitive membrane integration, local contrasts were obtained using stimuli down-sampled by averaging to 200 Hz. Local contrast distribution for the NS (black trace) was the narrowest, for the PN (blue trace) – the widest, and stimuli with partly randomized phase had intermediate distributions (red and green traces, Fig. 8A). These results, indicate that the NS, with very small local contrasts, are fully consistent with the ordering effects of HOC, which are prominently present in NS#3 as indicated by phase and entropy differentials (Table 1). Local contrast distributions for all NS and PN sequences are shown in Figure 8B, demonstrating that only a small fraction of NS had local contrast distributions as broad as those of PN sequences.

We can infer from Weber’s law that contrasts smaller than a certain undetermined Weber’s constant will not be reliably encoded by a photoreceptor, whereas larger contrasts will contribute to the output IR, with their number directly proportional to the bit rate. Indeed, strong positive Pearson’s correlations were found between the numbers of \textit{stimulus amplitude change events} exceeding a certain threshold value and the averaged output IRs for data obtained in the partial phase randomization experiment (Fig. 8C). Note that here the averaged rate consists of the averages of \(H\) and \(R\) values only, because all output \(E\) values were quite similar and actually tended to decrease with increasing HOC content (Table 4).

Using these statistical correlations, we attempted to estimate Weber’s constant for individual photoreceptors by gradually changing the threshold and evaluating the resulting correlations (Fig. 8D). We reasoned that if a threshold was too low, the Pearson’s correlations would be reduced due to the presence of low local contrast values not encoded by the photoreceptor and thus amounting to noise. If, on the other hand, a threshold was too high, the correlations would be distorted by a disproportional effect on the NS distribution characterized by high HOC content and small gradients (point-to-point value differences). Figure 8C shows three such correlations, and Figure 8D demonstrates Pearson product moment correlation coefficients for different thresholds. The Pearson correlation coefficient was used because the correlations between the number of stimulus amplitude change events and output bit rate were assumed to be linear. A clear maximum in correlation coefficients was detected at the threshold of 7% (Fig. 8C, D). When this threshold was applied to the distributions in Figure 8B, very strong positive correlations have emerged (Fig. 8E).

Figure 8F illustrates the aspects of NS/PN#3 stimulus pair that are expected to be encoded under the assumption of 7% local contrast threshold. For the 5-s trace segments shown, the “encodable” points are
presented in red. It can be seen that the PN segment contains more of such encodable events than the NS segment.

**Discussion**

Photoreceptors of vertebrates and invertebrates receive time-varying light intensity stimulation that is often strongly temporally predictable, or correlated in time, due to both time and space properties of natural scenes. In the frequency domain, this corresponds to input signals with strongly correlated phase relationships between different frequency components, or higher order correlations (HOC). Here, we searched for effects of such HOC on the transfer of information from light intensity to membrane potential in one type of insect photoreceptor. Although phototransduction and functioning of transduction ion channels are different in flies and mammals, overall similarities in neural connectivity in the retina and two peripheral neuropils in the fly, on one hand, and in the retina of vertebrates, on the other hand, established the fly as an important model organism for studying general principles of signal processing in the peripheral visual system (Fain et al. 2010; Sanes and Zipursky 2010; Kolodkin and Hiesinger 2017).

IRs calculated by three different methods produced consistent results: the more HOC a naturalistic stimulus (NS) included, the larger was the difference in the information transfer rates between the NS and the corresponding randomized phase stimulus (PN). These results are consistent with the hypothesis that photoreceptors do not discriminate between natural and random visual signals, at least regarding the amount of information they can transfer to the fluctuating membrane potential, and are not specifically evolutionary optimized to process natural light intensity time sequences.

Using partial phase randomization we confirmed that IR increased in both input and output as phase became progressively more random, and eliminated the possibility that correlations between input HOC proxies and output IR differences were due to some other properties of the stimuli. By analyzing the effects of mean stimulus intensity on output IRs, we demonstrated the crucial role of local contrast. Finally, we discovered strong positive correlations between local contrast integrals above a certain threshold value and output IRs. Comparison of correlations obtained by varying integration thresholds revealed a maximum at 7% of local contrast as the threshold for reliable detection of intensity changes, which can be interpreted as Weber’s constant for individual blowfly photoreceptors.

What does set this intensity resolution threshold in photoreceptors and how does it relate to other visual systems? Weber’s constant for the human visual system is 0.14 for rod and 0.02-0.03 for cone pathways, except for the S-cone pathway with a value of 0.09 (Stiles 1959; Davson 1990). In insect microvillar photoreceptors, the main limiting factor is probably the bump or transduction noise, originating from stochastic photon arrival (Lillywhite and Laughlin 1979). Bump noise decreases with light intensity
due to bump adaptation (Frolov et al. 2017). Here, responses to steady light stimuli showed that intensity corresponding to the mean stimulus amplitude of “1” (Table 1), gave standard deviations in de-trended responses from 0.5 to 1.5 mV for different cells (data not shown). Therefore, relatively small local contrasts in the stimulus eliciting responses of similar magnitudes will be transferred with high uncertainty, and smaller contrasts would not be discriminated at all. This sets the detection threshold in individual photoreceptors, and since NS sequences have narrower local temporal contrast distributions than PN sequences (Fig. 8B), explains the reduced IRs for NS.

Blowflies are dipterans, whose neural superposition mechanism sums six photoreceptor signals from the same spatial direction onto large monopolar cells (LMCs) in the lamina (Kirschfeld 1972; van Hateren 1987). This real-time averaging of input information can reduce noise 2.4-fold \((6^{0.5})\), increasing SNR and IR. As a result, small local contrasts, which might otherwise be missed by the visual system, can be detected, and the effective Weber’s constant in the lamina might be below 3\% \((7\%/2.4)\). Moreover, the 7\% threshold might be an overestimation of the blowfly photoreceptor Weber constant, since the mean stimulus amplitude was low (0.66 on the scale from 0 to 10 at ND0). Blowflies are normally active in daylight, where light intensities could substantially exceed the maximal intensity we used. This would further decrease transduction noise and improve resolution of small contrasts, decreasing the Weber’s constant. On the other hand, reduced light intensity would probably increase Weber’s constant.

Two of our other results deserve mention. First, lower IRs at the same photoreceptor depolarization levels make signals with high HOC content more expensive to process than their random-phase counterparts. Metabolic expenses are proportional to the number of K\(^+\) ions released by the photoreceptor through depolarization-activated K\(^+\) channels during graded voltage signaling (Laughlin et al. 1998; Niven et al. 2007). For the data shown in Figure 3, at the ND0 light intensity level, photoreceptors were on average depolarized by 20.2 ± 4.5 mV in response to NS#3 and by 19.4 ± 3.2 mV in response to PN#3. Since NS and PN in each pair produced responses with roughly the same mean depolarization, the cost of information contained in NS sequences increased proportionally with the amount of HOC. The more efficient processing of natural signals reported previously (Song and Juusola 2014) must be due to other factors than HOC.

Second, negative correlations between phase or entropy differentials and NS variance (Table 2) imply that natural stimuli with greater variability contain less HOC. This is counterintuitive because the more variable and feature-rich naturalistic sequences in the lower part of Figure 1 are usually perceived as typical “natural” sequences. However, as indicated by skewness (a measure of the asymmetry of the probability distribution function in respect to its mean) and kurtosis (a measure of outliers) values, NS with higher variance had much more symmetrical, Gaussian-like amplitude distributions than NSs with lower variance values (Table 1).
There is a broad agreement “that sensory neurons are tuned to efficiently encode natural stimuli” (Juusola and de Polavieja 2003; Friederich et al. 2016). However, visual neurons of vertebrates and invertebrates are organized in several consecutive neural centers, which in insects include retina and three optic neuropils: lamina, medulla and lobula. Processing of HOC could occur in any of one or more centers, and determining where and how it happens constitute important research questions. Unfortunately, virtually all studies on this topic in invertebrates were done using photoreceptors for the reason of experimental convenience. Studies of information processing in higher visual centers are complicated by difficulties in experimental access, poor stability of recordings, and, importantly, interpretation of mixed information coding as both graded signals and action potentials are used by higher-order neurons.

There is some consensus that photoreceptors process natural stimuli more efficiently than “unnatural” ones, based partly on studies comparing information transfer by photoreceptors stimulated by either natural/naturalistic or white-noise (WN) stimuli (Friederich et al. 2016), or by stimuli with altered phase distributions (Song and Juusola 2014). It has repeatedly been shown that some natural sequences elicit higher IRs than some WN sequences, and therefore suggested that nonlinear coding mechanisms of fly photoreceptors are tuned to suppress random phase signals (Friederich et al. 2016). However, comparison of WN and NS is difficult due to the profound differences in power spectrum distributions, which are linear in the former and have $1/f$ dependence in the latter. This difference is crucial since photoreceptor membranes are usually low-pass filters.

We failed to find any improved information transfer by individual photoreceptors transducing inputs with high-order statistical correlations such as those in natural signals. Instead, HOC reduced local intensity gradients and contrasts, and diminished the detectable intensity changes in the stimulus. This was reflected in relatively low entropies of both stimuli with high HOC content and the corresponding photoreceptor responses. Individual blowfly photoreceptors faithfully transfer intensity changes that exceed the noise-imposed threshold, regardless of local phase structure. It seems likely that information about phase is not encoded in the activity of individual photoreceptors but rather in the characteristic temporal patterns of visual flow from patches of the retina exposed to the same visual scene, and extracted by neurons in higher-order visual centers. While these data were based on one invertebrate visual system, it will be important to test this hypothesis in other animals, including vertebrates.

**Author contributions**

Irina I. Ignatova and Roman V. Frolov conceived and designed the experiments; Irina I. Ignatova performed experiments; Irina I. Ignatova and Roman V. Frolov analyzed data. All authors discussed findings, provided critical input, wrote, edited and approved the manuscript, and agree to be accountable for all aspects of the
work. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

**Funding**

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**References**


**Figure legends**
Figure 1. Inputs in time domain. Typical pairs of matching naturalistic (NS, black traces) and randomized phase pink noise stimuli (PN, grey traces) are shown together with their Fourier phase spectra and normalized amplitude distribution histograms; the stimulus amplitude range is 0-10; ten out of forty stimulus pairs are shown; for presentation purposes NS and PN histograms were normalized independently so that the areas under the curves are not equal; numbering of stimuli is explained in Figure 2D. For three stimulus pairs, NS/PN#1, 24, and 39, the full-length stimuli are also shown as single-pixel arrays; for this presentation, signals were first down-sampled to 200 Hz and then the stimulus amplitude 0-10 range was converted to the 0-255 gray-scale pixel range.

Figure 2. Entropy and phase of the matched input pairs. (A) One-sided Fourier amplitude spectra for all forty pairs of matching NS and PN stimuli. The traces for each pair coincide completely. (B) One-sided unwrapped phase spectra of NS (main plot) and the corresponding PN stimuli (inset); PN stimuli are characterized by very low phase values due to randomization. (C) Input stimuli NS #20 and PN #20 are shown together with the momentary $E$ rates (lower part); entropy was determined in 1-s intervals. (D) Compression entropy values for the pairs of matching NS and PN stimuli (see Methods for details); the pairs are ordered according to the increasing difference in entropy within the pair; the numbers are the same throughout the article. (E) Correlation between differences in absolute phases (at 200 Hz) and compression entropy for each pair of stimuli; the Spearman’s $\rho$ value was statistically significant ($P < 10^{-6}$).

Figure 3. Analysis of responses to NS/PN#3 stimulus pair. (A, B) Typical responses of one photoreceptor to NS#3 and PN#3, respectively, obtained at four light levels in ten-fold intensity increments, from dark grey to blue. (C) Power spectra of stimuli (black for NS and dark gray for PN) overlap completely. Power spectra of responses from panels A and B at ND0. (D, E) Gain (D), and SNR (E) functions at ND0 for responses in panels A and B. (F-K) Analysis of information transfer by three methods, coherence rate $H$ (F, I), mutual information $R$ (G, J), and entropy $E$ (H, K) for the entire experimental group; circles and triangles denote PN and NS responses, respectively; color indicates light intensity as in panels I-K; F-H show dependence of IRs on membrane depolarization, and I-K – on the nominal neutral density (ND) filter group; here and elsewhere values are mean ± s.d.

Figure 4. Information rates of outputs. Correlations between input phase or entropy differentials within each pair of stimuli and average normalized differences in output IRs determined using the coherence (A, B), mutual information (C, D), and compression entropy (E, F) methods. (G, H) Correlations between the input phase (G) and entropy (H) differentials and relative differences in combined output IRs. Combined output IRs were calculated by averaging the values of average relative differences in output IRs obtained using each of the three methods. All IRs were obtained from photoreceptor responses at the brightest light level ND 0; the number of cells for each pair of stimuli varied from 4 to 7.
Figure 5. Partial phase randomization. (A) Inputs (shown to the half of their maxima) and the corresponding photoreceptor responses illustrate effects of increasing phase randomization, from a naturalistic stimulus with an intact Fourier phase spectrum (upper trace), to a stimulus with original phase preserved by 75% (25% PN, black trace), or 25% (75% PN, second trace from below), and to PN (lower trace); insets show 4-Hz segments of phase spectra, with intact and randomized phase segments as denoted (see Methods for details); inputs have the same amplitude spectra; responses were evoked at the brightest light intensity (ND0). (B) The corresponding phase spectra. (C) Input compression entropy rates. (D-F) Output rates $H$, $R$, and $E$, respectively for two photoreceptors.

Figure 6. Effects of background on information rate of NS#31. Panel A shows three inputs with different background intensities and the corresponding representative responses obtained at ND0; black trace is NS#31, which is characterized by the highest variability (Fig. 4B); grey and dark grey traces are the same but with lower baselines; numbers to the right of the stimuli indicate the lowest amplitudes (“background intensities”) in the stimuli; color coding is the same for the responses shown. (B-D) Gain (B), coherence (C), and SNR (D) functions; traces are averages from responses of three photoreceptors. (E) Dependencies of output rates $H$, $R$, and $E$ on the stimulus background; the numbers are the mean contrasts.

Figure 7. Effects of mean stimulus amplitude on information rate and information rate differentials. (A, B) The NS (A) and PN (B) stimuli created on the basis of NS/PN#3 with different mean amplitudes (0.04, 0.24, and 1.04) are shown together with typical responses; panel A shows only three out of six NS and two out of five PN used in these experiments; no matching PN sequence could be made for the NS with the mean amplitude 0.04; color coding is the same for the responses shown. (C-E), Gain (C), coherence (D), and SNR (E) functions are shown for the same responses as in panels A and B. (F-H), Dependencies of output rates $H$ (F), $R$ (G), and $E$ (H) on mean stimulus amplitude; numbers in G are the corresponding values of mean contrast; (n) in H are the numbers of experiments. (I), Effects of the mean stimulus amplitude on the averaged IR differential $(IR_{PN} - IR_{NS})/IR_{PN}$ (see Results).

Figure 8. Local contrasts and information rates. (A) Local contrast distributions for four stimuli used in randomized phase experiments (Fig. 5A): NS, a 75% NS, a 25% NS, and PN; local contrasts were calculated as the intensity gradient divided by the previous intensity value, $(I_{n+1} - I_{n})/I_{n}$. (B) Local contrast distributions for all forty pairs of NS (blue) and PN (red) sequences; dashed lines show an example of a threshold. (C) Correlations between the local contrast integrals and average output IRs; the integrals were obtained by summing the contrast distributions from panel A above a threshold varying from 1% to 17% (in this panel, correlations for 4%, 7%, and 10% thresholds are shown); the output rates are averages of mean $H$ and $R$ values from Fig. 9D, E. (D) Dependence of the correlation coefficient on the threshold value for data in panel A. (E) Correlations between the local contrast integrals above the 7% threshold for all distributions
from panel B and average output IRs. (F) 5-s fragments of NS#3 and PN#3 with red indicating points characterized by local contrast values exceeding 7%.

Tables

Table 1. Statistical properties of stimuli

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21
The “original NS mean ampl.” stands for the mean amplitude of the natural sequences used to construct the NS/PN stimuli pairs (see Methods). The amplitude spectrum integral was obtained from data shown in Figure 2A by integrating values in the range from 1 to 100 Hz, and reflects the stimulus variance in the frequency domain.

**Table 2. Spearman’s rank order correlation coefficients for correlations between input parameters**

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<tr>
<td>Standard deviation</td>
<td>-0.78 (10⁻⁵)</td>
<td>-0.62 (10⁻⁵)</td>
<td>0.98 (10⁻⁶)</td>
<td>0.84 (10⁻⁶)</td>
<td>0.91 (10⁻⁵)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean contrast</td>
<td>-0.24 (0.14)</td>
<td>-0.11 (0.49)</td>
<td>0.34 (0.032)</td>
<td>0.33 (0.036)</td>
<td>0.30 (0.058)</td>
<td>0.51 (8·10⁻²)</td>
<td></td>
</tr>
</tbody>
</table>

Numbers in parentheses in this and other tables indicate $P$ values.

**Table 3. Response information rates**

<table>
<thead>
<tr>
<th>#</th>
<th>Entropy rate, bits s⁻¹</th>
<th>Coherence rate, bits s⁻¹</th>
<th>Mutual information rate, bits s⁻¹</th>
<th>#</th>
<th>Entropy rate, bits s⁻¹</th>
<th>Coherence rate, bits s⁻¹</th>
<th>Mutual information rate, bits s⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NS</td>
<td>PN</td>
<td>NS</td>
<td>PN</td>
<td>NS</td>
<td>PN</td>
<td>NS</td>
</tr>
<tr>
<td>1</td>
<td>426±24</td>
<td>470±23</td>
<td>107±9</td>
<td>215±16</td>
<td>38±3</td>
<td>62±4</td>
<td>211±27</td>
</tr>
<tr>
<td>2</td>
<td>425±41</td>
<td>482±14</td>
<td>104±20</td>
<td>304±35</td>
<td>24±4</td>
<td>46±7</td>
<td>22±24</td>
</tr>
<tr>
<td>3</td>
<td>414±18</td>
<td>460±11</td>
<td>138±12</td>
<td>239±27</td>
<td>62±1</td>
<td>70±3</td>
<td>23±30</td>
</tr>
<tr>
<td>4</td>
<td>408±28</td>
<td>444±20</td>
<td>49±12</td>
<td>124±30</td>
<td>30±5</td>
<td>74±5</td>
<td>24±24</td>
</tr>
<tr>
<td>5</td>
<td>419±19</td>
<td>502±22</td>
<td>143±21</td>
<td>327±59</td>
<td>50±2</td>
<td>54±4</td>
<td>25±30</td>
</tr>
<tr>
<td>6</td>
<td>386±10</td>
<td>437±22</td>
<td>61±5</td>
<td>120±10</td>
<td>19±1</td>
<td>64±3</td>
<td>26±30</td>
</tr>
<tr>
<td>7</td>
<td>435±15</td>
<td>499±22</td>
<td>153±39</td>
<td>312±80</td>
<td>47±24</td>
<td>52±3</td>
<td>27±30</td>
</tr>
<tr>
<td>8</td>
<td>395±13</td>
<td>433±16</td>
<td>100±6</td>
<td>147±18</td>
<td>52±4</td>
<td>84±7</td>
<td>28±30</td>
</tr>
<tr>
<td>9</td>
<td>406±10</td>
<td>468±11</td>
<td>152±13</td>
<td>262±25</td>
<td>43±2</td>
<td>53±3</td>
<td>29±30</td>
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<tr>
<td>10</td>
<td>407±26</td>
<td>472±12</td>
<td>218±22</td>
<td>316±38</td>
<td>50±4</td>
<td>57±4</td>
<td>30±30</td>
</tr>
<tr>
<td>11</td>
<td>412±25</td>
<td>454±22</td>
<td>68±28</td>
<td>168±96</td>
<td>46±6</td>
<td>63±5</td>
<td>31±30</td>
</tr>
<tr>
<td>12</td>
<td>426±14</td>
<td>481±16</td>
<td>147±14</td>
<td>272±36</td>
<td>48±2</td>
<td>61±3</td>
<td>32±30</td>
</tr>
<tr>
<td>13</td>
<td>413±8</td>
<td>473±3</td>
<td>167±23</td>
<td>321±43</td>
<td>47±3</td>
<td>57±1</td>
<td>33±30</td>
</tr>
</tbody>
</table>

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Table 4. Correlations between input and response parameters

<table>
<thead>
<tr>
<th>Response</th>
<th>( \frac{E_{PN} - E_{NS}}{E_{PN}} ), bits s(^{-1} )</th>
<th>( \frac{H_{PN} - H_{NS}}{H_{PN}} ), bits s(^{-1} )</th>
<th>( \frac{R_{PN} - R_{NS}}{R_{PN}} ), bits s(^{-1} )</th>
<th>Mean amplitude ( E_{PN} - E_{NS} ), bits s(^{-1} )</th>
<th>Mean contrast ( \Phi_{PN} - \Phi_{NS} ), rad</th>
</tr>
</thead>
<tbody>
<tr>
<td>Input</td>
<td>( \frac{E_{PN} - E_{NS}}{E_{PN}} ), bits s(^{-1} )</td>
<td>( \frac{H_{PN} - H_{NS}}{H_{PN}} ), bits s(^{-1} )</td>
<td>( \frac{R_{PN} - R_{NS}}{R_{PN}} ), bits s(^{-1} )</td>
<td>Mean amplitude ( E_{PN} - E_{NS} ), bits s(^{-1} )</td>
<td>Mean contrast ( \Phi_{PN} - \Phi_{NS} ), rad</td>
</tr>
<tr>
<td>14</td>
<td>403±12</td>
<td>432±16</td>
<td>127±5</td>
<td>0.74 (10(^{-6}))</td>
<td>0.68 (10(^{-6}))</td>
</tr>
<tr>
<td>15</td>
<td>435±12</td>
<td>492±13</td>
<td>154±17</td>
<td>0.84 (10(^{-6}))</td>
<td>0.73 (10(^{-6}))</td>
</tr>
<tr>
<td>16</td>
<td>413±6</td>
<td>448±11</td>
<td>121±13</td>
<td>0.65 (10(^{-5}))</td>
<td>0.51 (10(^{-3}))</td>
</tr>
<tr>
<td>17</td>
<td>426±14</td>
<td>477±32</td>
<td>99±10</td>
<td>0.50 (10(^{-2}))</td>
<td>0.25 (0.12)</td>
</tr>
<tr>
<td>18</td>
<td>439±6</td>
<td>473±25</td>
<td>188±16</td>
<td>0.27 (0.1)</td>
<td>0.07 (0.65)</td>
</tr>
<tr>
<td>19</td>
<td>387±12</td>
<td>396±9</td>
<td>97±8</td>
<td>-0.64 (10(^{-5}))</td>
<td>0.05 (0.8)</td>
</tr>
<tr>
<td>20</td>
<td>400±12</td>
<td>425±15</td>
<td>72±19</td>
<td>-0.65 (10(^{-5}))</td>
<td>-0.04 (0.8)</td>
</tr>
</tbody>
</table>
Figure 1.
Figure 3

A NS #3

B PN #3

C Normalized input power

D Response power (mV)

E SNR

F H (bits s⁻¹)

G R̂ (bits s⁻¹)

H Ê (bits s⁻¹)

I H (bits s⁻¹)

J R̂ (bits s⁻¹)

K Ê (bits s⁻¹)
Figure 4

A. $\rho = 0.73$

B. $\rho = 0.84$

C. $\rho = 0.51$

D. $\rho = 0.65$

E. $\rho = 0.68$

F. $\rho = 0.74$

G. $\rho = 0.78$

H. $\rho = 0.91$
Figure 5

A

inputs

voltage responses

a 4-Hz segment

\( \Phi_{\text{input}} (\text{Hz}) \)

100% NS

25% PN

75% PN

100% PN

B

\( \phi_{\text{input}} \) (rad x 10^4)

Frequency (Hz)

1 10 100

100% NS
25% PN
75% PN
100% PN

C

\( E_{\text{input}} \) (bits s^-1)

Random phase (%)

0 25 50 75 100

D

\( H_{\text{output}} \) (bits s^-1)

Random phase (%)

0 25 50 75 100

cell 1

cell 2

E

\( R_{\text{output}} \) (bits s^-1)

Random phase (%)

0 25 50 75 100

cell 1
cell 2

F

\( E_{\text{output}} \) (bits s^-1)

Random phase (%)

0 25 50 75 100

cell 1
cell 2
Figure 6

A

inputs

NS3.46 responses

NS1.73

5 s

NS0

B

Gain (mV)

Frequency (Hz)

C

Coherence

NS3.46

NS1.73

NS0

Frequency (Hz)

D

SNR

Frequency (Hz)

E

Information (bits s⁻¹)

Background

1.53

0.54

0.33

H

R

29
Figure 7

A. Inputs and responses for different conditions.
B. Comparison of inputs and responses for NS0.24 and PN0.24.
C. Gain vs. frequency for NS0.04, NS0.24, NS1.04, PN0.24, PN1.04.
D. Coherence vs. frequency for different conditions.
E. SNR vs. frequency for different conditions.
F. Mean amplitude vs. throughput for NS and PN.
G. Mean amplitude vs. throughput for NS and PN.
H. Mean amplitude vs. throughput for NS and PN.
I. IR differential vs. mean amplitude for NS and PN.
Figure 8