



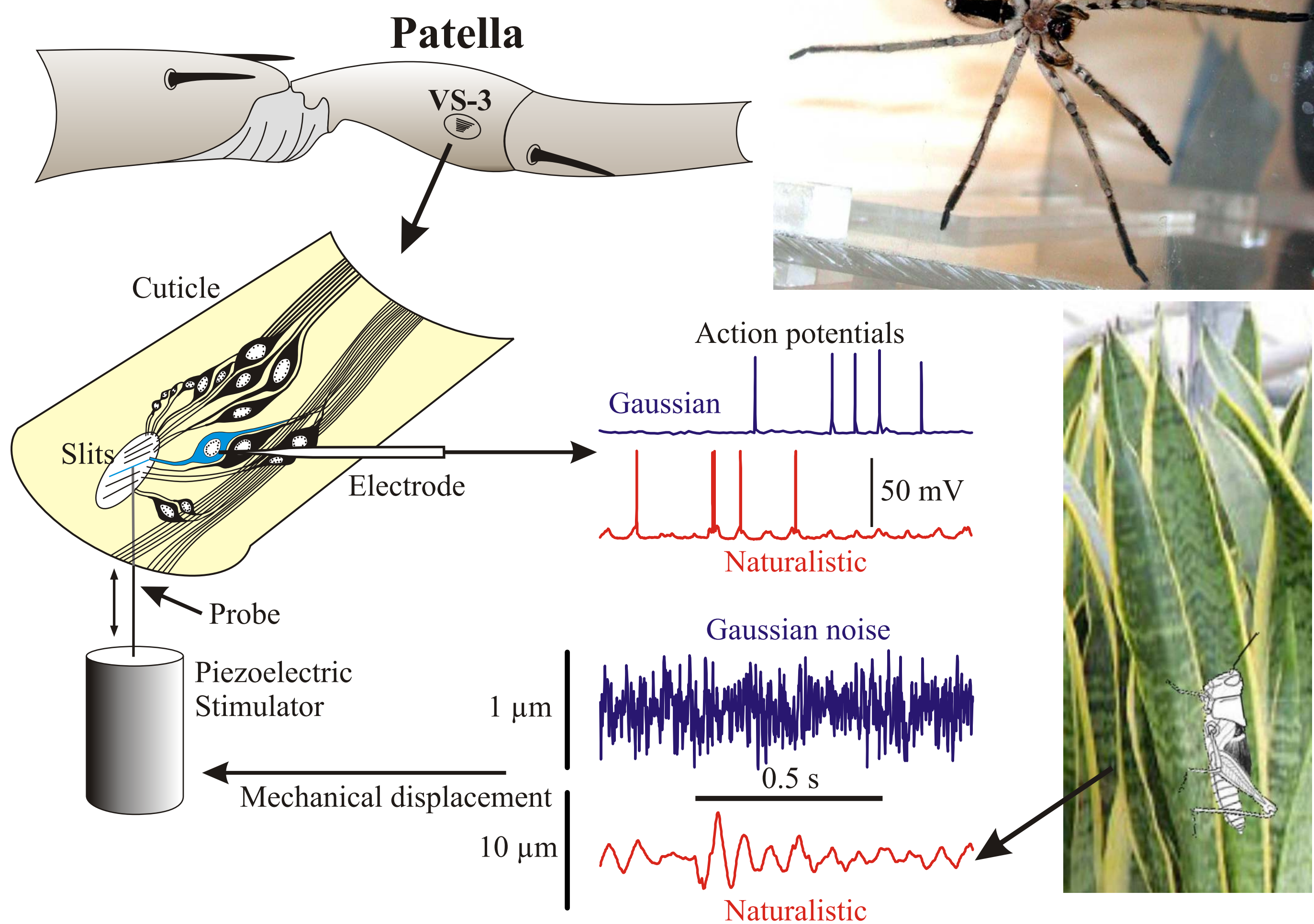
Naturalistic stimulation increases high frequency sensitivity in spider mechanosensory neurons

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1. Mechanical stimulation of VS-3 Organ

The VS-3 slit organ of *Cupiennius salei* has 14-16 neurons in the patellar hypodermis that innervate 7-8 slits in the patella. They can be penetrated by microelectrodes to observe mechanotransduction while the slits are moved from below.



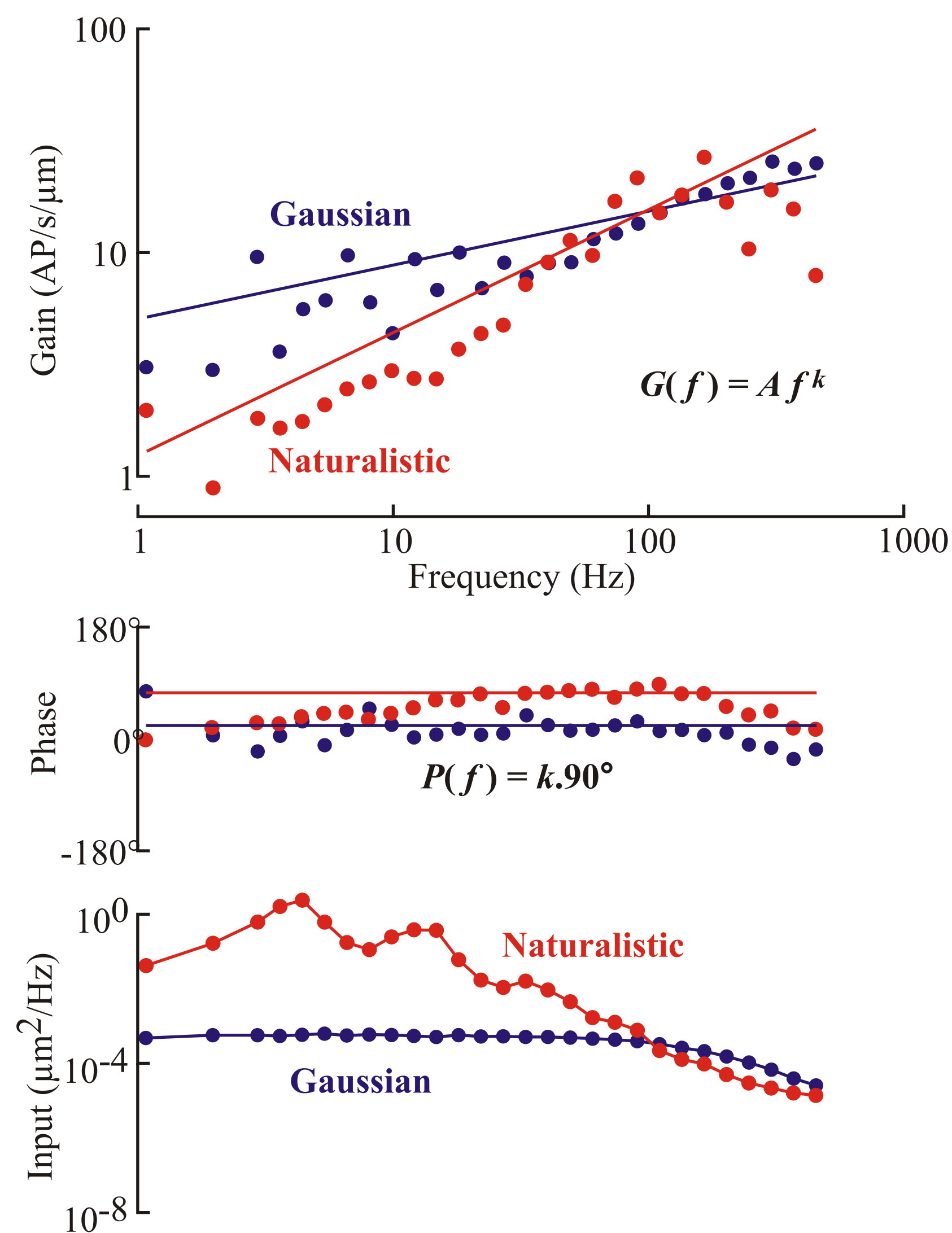
- Naturalistic signal was generated by 5th instar *Schistocerca gregaria* walking up a *Sansevieria* plant, while leaf vibration was observed using laser Doppler vibrometry.
- Gaussian noise amplitude was adjusted to give the same firing rate as the naturalistic stimulation (means: 5.46 ± 2.63 AP/s (naturalistic) and 6.06 ± 4.09 AP/s (Gaussian), $n=11$).

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2. Linear frequency responses



Naturalistic stimulation caused increasing sensitivity to higher frequency inputs (increased values of k).

Linear frequency responses were fitted by the power law (Equations for gain and phase are shown).

Mean fitted parameters to the gain and phase from 11 experiments were:

$k = 0.26, A = 24.2$ AP/s/μm (Gaussian)

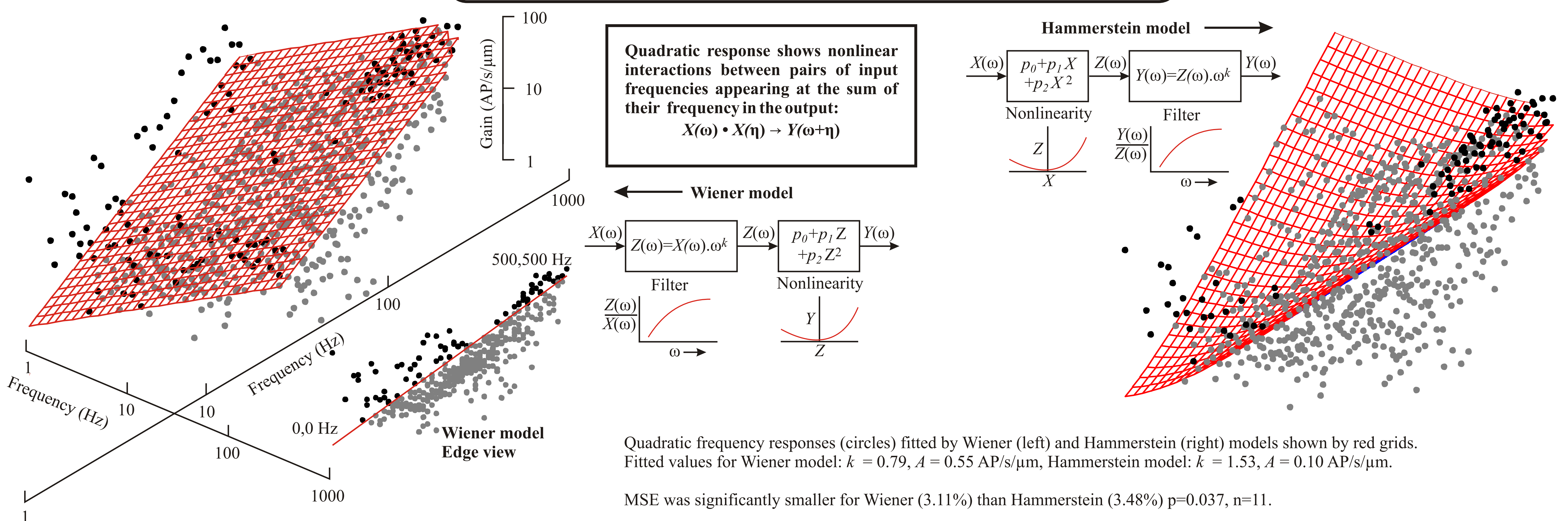
$k = 0.57, A = 2.5$ AP/s/μm (Naturalistic)

The Gaussian stimulus had an almost flat frequency distribution.

The naturalistic stimulus was stronger at low frequencies, with peaks at ~4 Hz and ~10 Hz.

The mechanical stimulator response declined slowly above ~70 Hz. A sharp low pass filter cut all signals above 300 Hz.

3. Quadratic frequency response to naturalistic stimulation



Quadratic response shows nonlinear interactions between pairs of input frequencies appearing at the sum of their frequency in the output:
 $X(\omega) \cdot X(\eta) \rightarrow Y(\omega+\eta)$

Wiener model

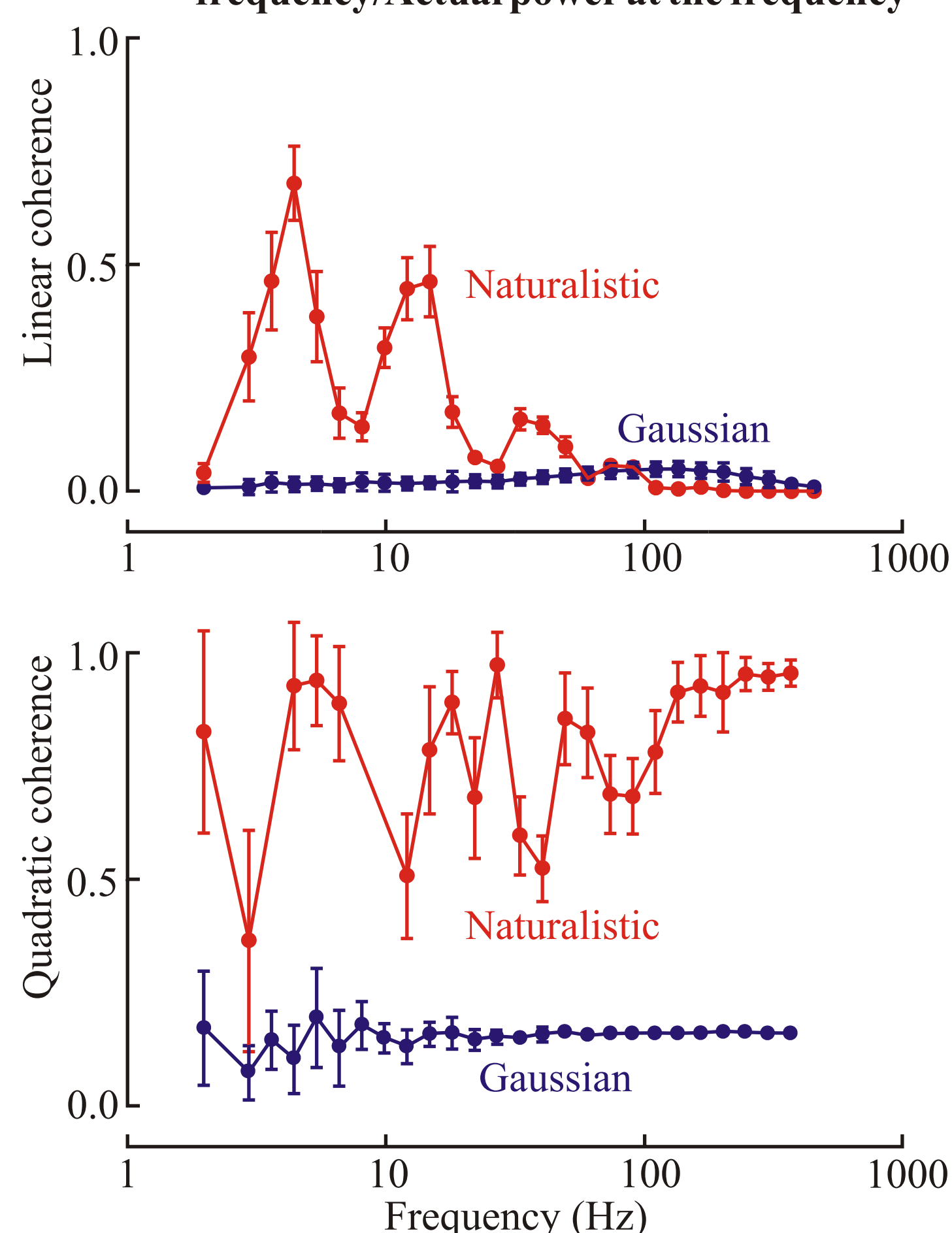
Hammerstein model

Quadratic frequency responses (circles) fitted by Wiener (left) and Hammerstein (right) models shown by red grids. Fitted values for Wiener model: $k = 0.79, A = 0.55$ AP/s/μm, Hammerstein model: $k = 1.53, A = 0.10$ AP/s/μm.

MSE was significantly smaller for Wiener (3.11%) than Hammerstein (3.48%) $p=0.037, n=11$.

4. Naturalistic stimulation increases nonlinearity

Coherence = Predicted output power at a frequency/Actual power at the frequency



- Naturalistic stimulation raised linear coherence at low vs high frequencies.
- Quadratic coherence was higher than linear coherence for both naturalistic and Gaussian stimulation (nonlinearity).
- Peak frequencies were shifted in quadratic coherence (nonlinearity).

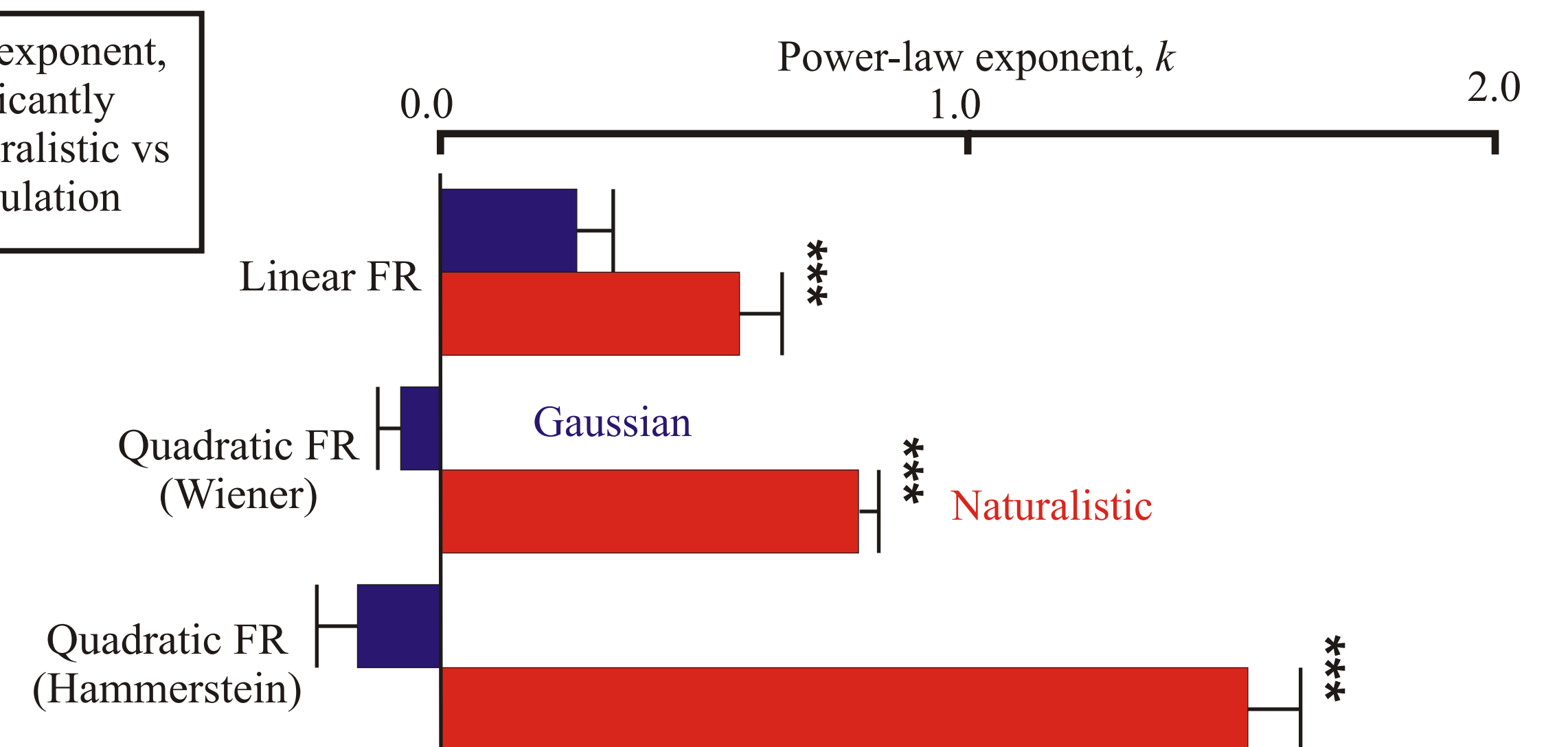
- Linear coherence:
 $\gamma^2(\omega) = \frac{\langle |Y(\omega)X(\omega)^*|^2 \rangle}{\langle X(\omega)X(\omega)^* \rangle \langle Y(\omega)Y(\omega)^* \rangle}$

where X, Y are input and output Fourier components of frequency, $\omega, >$ indicates an ensemble average, and $*$ a complex conjugate.

- Quadratic coherence, $\phi^2(\mu)$:
 $B^2(\omega, \nu) = \frac{\langle |K_2(\omega, \nu)X(\omega)X(\nu)|^2 \rangle}{\langle |Y(\omega+\nu)|^2 \rangle}$
and,
 $\phi^2(\mu) = \int B^2(\omega, \mu-\omega) d\omega$
where $K_2(\omega, \nu)$ is the quadratic frequency response and ω, ν, μ are all frequencies.

5. Naturalistic stimulation increases exponent, k

All measures of exponent, k , were significantly higher with Naturalistic vs Gaussian stimulation



6. Conclusions

- Naturalistic stimulation changed the linear and quadratic responses to transmit the low frequency peaks in the input signal.
- A model containing a linear filter followed by a strong nonlinearity was most favored, but the system is clearly more complex than this simple model.
- Quadratic coherence indicates strongly nonlinear behavior, even with Gaussian stimulation. It is more evident with Naturalistic stimulation.