# NATURAL SCENE STATISTICS AND NONLINEAR NEURAL INTERACTIONS BETWEEN FREQUENCY-SELECTIVE MECHANISMS

*Christoph Zetzsche and Ulrich Nuding*
Institut für Medizinische Psychologie, Ludwig-Maximilians-Universität München
Goethestr. 31, D-80336 München, Germany
chris@imp.med.uni-muenchen.de

## ABSTRACT

Linear filtering is a central concept in many modeling approaches to neural information processing. In particular the sensory systems for vision and audition have been successfully described as multi-channel systems which consist of independent and frequency-selective linear filter mechanisms. Further support for the existence of such linear filters came from recent investigations of the optimal neural transforms for the exploitation of natural scene statistics [1][2]. However, more detailed investigations revealed the existence of substantial statistical dependencies that would remain between the responses of independent linear filters, and suggest that if the sensory systems are really optimal there should exist substantial nonlinear interactions between the filters [2][3]. These results pose two questions for the understanding of neural sensory infromation processing: (i) What are suitable nonlinear interactions? and (ii) Why have such nonlinear interactions never been observed in the vast number of neurophysiological investigations?

Let us consider the visual system as an example for the investigation of these two questions. Here the classical view is that the early visual processing is performed by a set of linear frequency-selective filter mechanisms with different preferred spatial frequencies. However, if we consider the joint responses of such linear filters to natural images, we find that these responses are statistically dependent (Fig. 1). This is mainly due to edges in the images, since filter mechanisms with different preferered spatial frequencies are jointly activated at the position of the edge (cf. Fig. 2a-c). This statistical property cannot be exploited by any linear mechanism but requires nonlinear interactions that realize a nonlinear, AND-like combination of frequency components.

To understand this, let us consider the basic logical gating functions that can be provided by the linear and the nonlinear combinations of two variables $r_1$,$r_2$. For this, we distinguish only between insignificant and significant values (close to zero and non-zero values), and denote them by 0 and I.

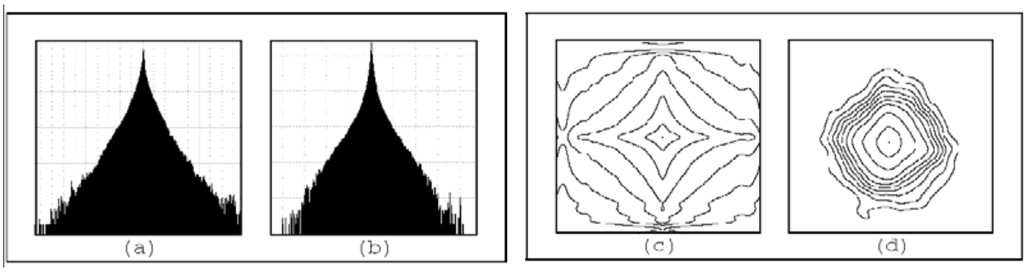

**Figure 1: Statistical dependencies between linear frequency-selective filters (adapted from [3]). The response statistics p($r_1$) and p($r_2$) of two mechanisms with different preferred spatial frequencies $f_1$ and $f_2$ are shown in (a),(b). If the responses would be statistically independent the joint statistics p($r_1$,$r_2$) should equal p($r_1$)p($r_2$). The resulting iso-level curves of the independent p($r_1$,$r_2$) are shown in (c). The actual joint statistics p($r_1$,$r_2$) are shown in (d), and are clearly different. This implies that linear filters would yield responses with substantial statistical dependencies.**

The linear summation $r_1+r_2$. then corresponds to a logical OR (00 →0 ; 0I, I0, II →I). A logical AND can be obtained by the product $r_1r_2$ , which is a nonlinear operation (00, 0I, I0 →0 ; II →I). (It should be noted that multiplication is of course only one among many possibilities for the realization of an analog AND operation, and is used here only for convenience).

Such a nonlinear AND combination can be used for a neural mechanism that yields a large response at only those locations at which both linear filters are activated, and yields no significant response at the locations at which only one of the two filters is activated. Let us consider the simple multiplication of the two linear filter responses $r_1$ and $r_2$ (Fig. 2d). It is interesting to note that the resulting response $r_N=r_1r_2$ appears not extremely nonlinear on a first look. Without knowing about the nature of the nonlinearity it may well be interpreted as response of a linear filter. A similar effect results with the responses to sinusoidal gratings (Fig. 2h), and based on the responses to such sinusoids with different spatial frequencies one can determine a classical spectral tuning function $S_N(f)$ of the nonlinear system, which has the typical bandpass shape encountered in electrophysiological investigations of cortical visual neurons (Fig. 2h).

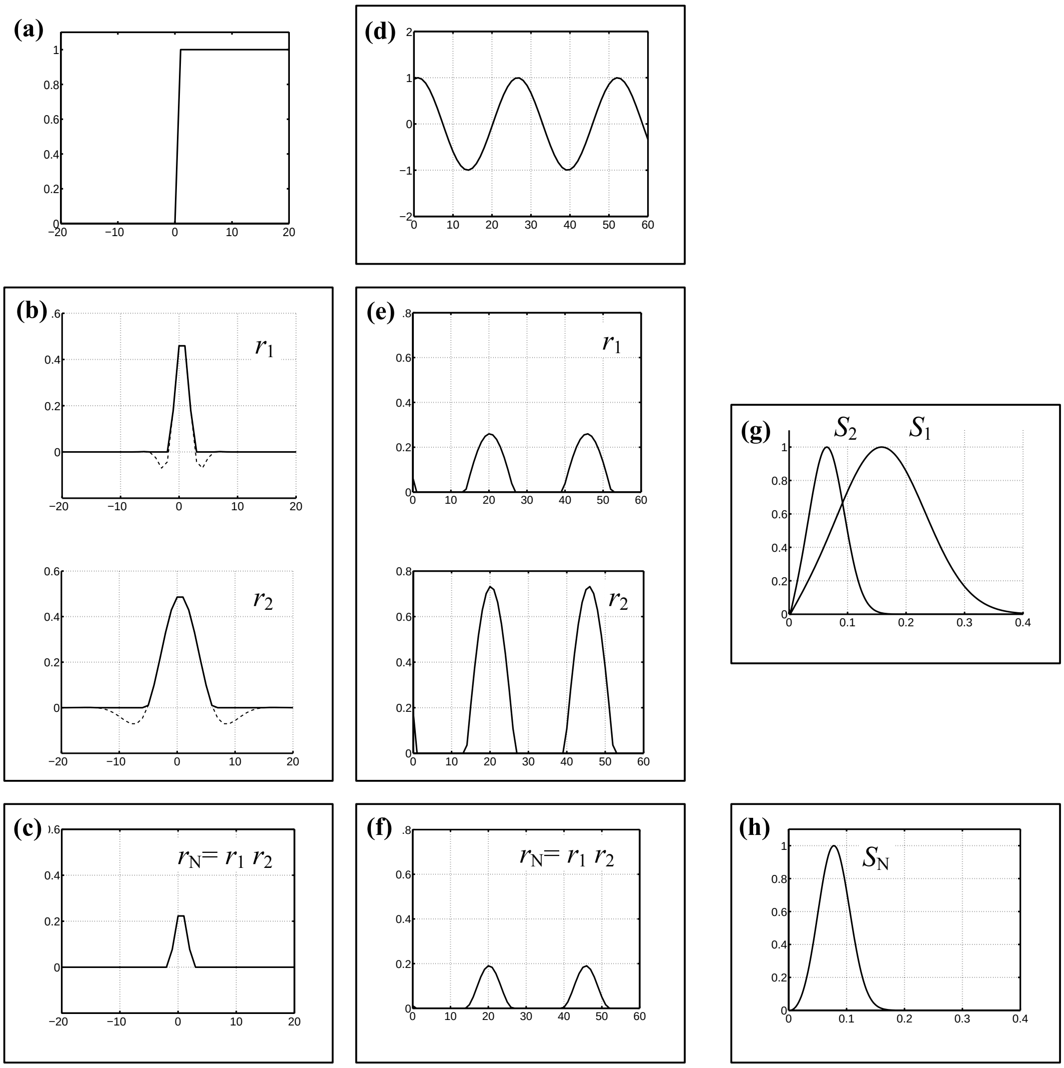

**Figure 2: (a) Step (edge) input. (b) Responses $r_1$ and $r_2$ of two linear filters with different preferred spatial frequencies. (Since spikerates cannot become negative only the positive ("ON") responses are used in all simulations.) (c) Nonlinear response $r_N$ resulting from a multiplicative (AND like) combination of $r_1$ and $r_2$. (d-f) Linear responses and resulting nonlinear response for a sinusoidal input. (g) Spectral tuning functions $S_1(f)$,$S_2(f)$ of the two linear filters. (h) Spectral tuning function $S_N(f)$ of the nonlinear AND system as measured with sinusoidal inputs.**

These examples demonstrate that it is easily possible that substantial nonlinearities of neural responses may be overlooked if there exists no clear concept of the nature of the nonlinearity in the experiments. However, once the appropriate concept exists, it is of course possible to devise tests which clearly reveal the nonlinear behavior. The straightforward test for an AND combination of frequency-selective mechanisms is by the presentation of two superimposed sinusoids (Fig. 3). The frequencies can be chosen to yield a significant activation of the component filters of the nonlinear system, while falling at the same time almost outside the passband of the presumed "linear" filter function $S_N(f)$ of the system (Fig. 3a-c). For a system with this filter function the low-frequency sinusoid will yield only a weak response, and the high-frequency sinusoid will yield almost no response at all (Fig. 3d). For a truly linear system, the response to the combination should equal the sum of the responses to the components: $r_L[e_A+e_B]=r_L[e_A]+r_L[e_B]$. It should hence have about the size and shape of the weak response (Fig. 3e).

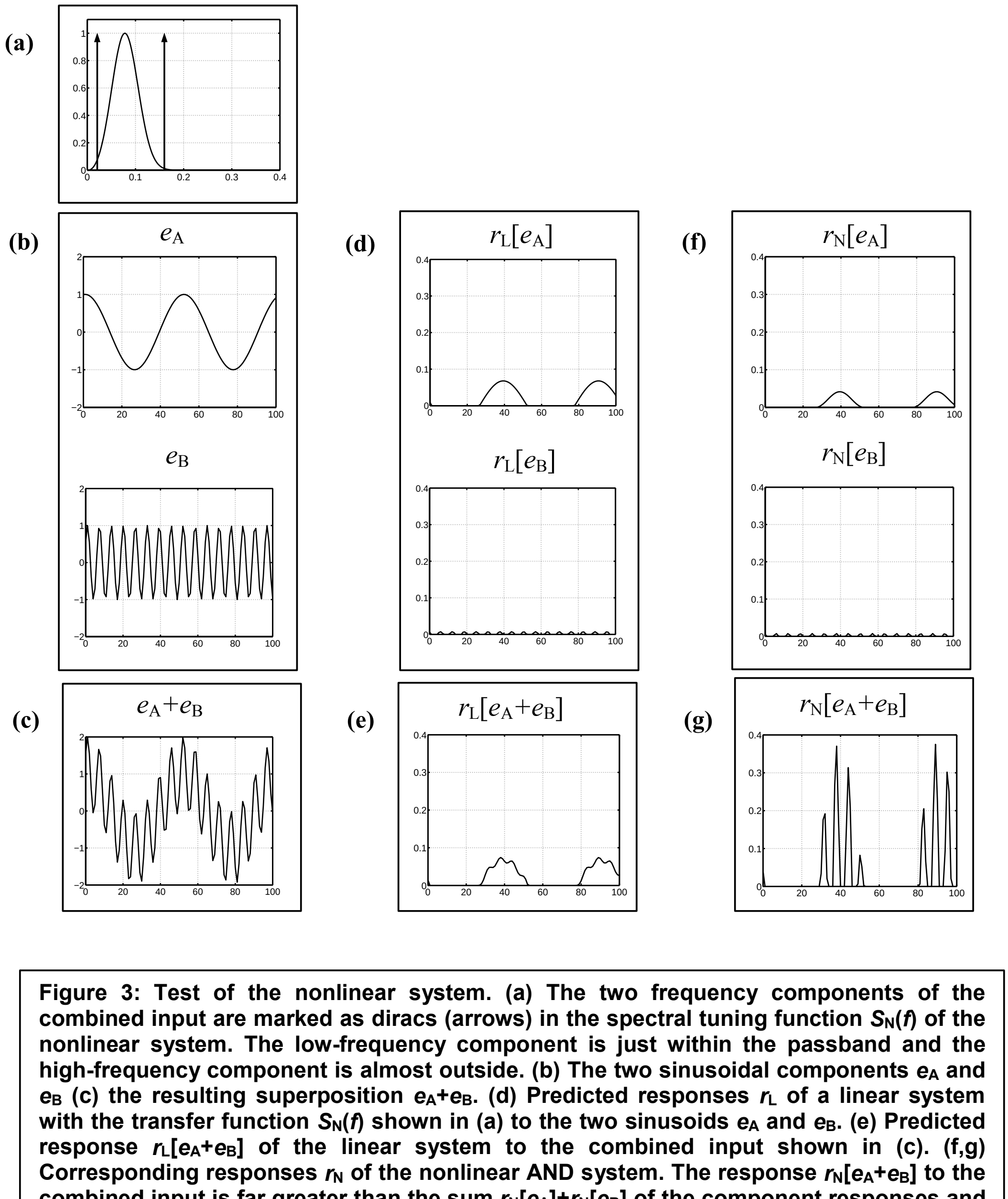

**Figure 3: Test of the nonlinear system. (a) The two frequency components of the combined input are marked as diracs (arrows) in the spectral tuning function $S_N(f)$ of the nonlinear system. The low-frequency component is just within the passband and the high-frequency component is almost outside. (b) The two sinusoidal components $e_A$ and $e_B$ (c) the resulting superposition $e_A+e_B$. (d) Predicted responses $r_L$ of a linear system with the transfer function $S_N(f)$ shown in (a) to the two sinusoids $e_A$ and $e_B$. (e) Predicted response $r_L[e_A+e_B]$ of the linear system to the combined input shown in (c). (f,g) Corresponding responses $r_N$ of the nonlinear AND system. The response $r_N[e_A+e_B]$ to the combined input is far greater than the sum $r_N[e_A]+r_N[e_B]$ of the component responses and has a additionally a substantially different structure as the linear prediction.**

However, this linear superposition rule will be dramatically violated by the nonlinear AND system: we take a signal $e_A$ which yields only a weak response, we add to this a second signal $e_B$ which for itself yields no reponse at all, and we obtain a response to this combined input which drastically exceeds the sum of the respones to the component signals ( $r_N[e_A+e_B]>>r_N[e_A]+r_N[e_B]$), and which additionally has an entirely different shape (Fig.3g). But this effect is only surprising from the viewpoint of linear filter theory. From the viewpoint of a nonlinear AND combination, it is quite straightforward: Neither the low-frequency component alone (I0) nor the high-frequency component alone (0I) can yield a significant output (0I,I0 →0). The AND is only activated by the joint presence of both components (II →I).

The simulations presented in this paper should be regarded as qualitive illustration of the nonlinear interactions that should be expected in principle, rather than as exact quantitative prediction. In order to derive such a quantitative prediction much more details have to be known, e.g. about the type of AND operation that can realized in neural circuits. Multiplication is mathematically simple but whether it can be easily implemented neurally, or whether it is functionally the most desirable version of an analog AND operation remains to be determined. (A more general version can for example be obtained by $f(|r_1+r_2|)$ - $f(|r_1-r_2|)$, where $f$ can be any even-symmetric function. Then $f(.)=(.)^2$ yields the product, and $f(.)=|\ .\ |$ yields $\min(r_1,r_2)$, which is another example of the class of analog AND operations. Sigmoid $f$'s are also possible.) Furthermore, the prediction depends on the detailed type of neurophysiological measurement. In many experiments only the response energy of the fundamental harmonic is measured and all higher harmonics are discarded. Such a strategy is severely biased towards a linear interpretation, since the strongest nonlinear effects have to be expected in the higher harmonics (cf. Fig. 3e,g). An actual increase in the response amplitude may even correspond to a decrease of the fundamental harmonic if the spectral composition of the response changes. However, irrespective of the details we would insist on a critical structural prediction: there should exist neurons in the visual system for which the response to superimposed gratings consisting of frequencies far away from the “preferred” frequency of the neuron (as given by its “linear” filter function) differs drasticallly from the superposition of the responses to the individual frequency components. Such a behavior would indeed be an efficient strategy for the exploitation of the statistical redundancies of the natural environment.

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