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Non-Linear Analysis of the Transmission of Signals in the Auditory System of the Migratory Locust *Locusta Migratorta**

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Abstract. Investigations on the auditory system of the migratory locust using the system theory (i.e. the white-noise method) to determine the transfer characteristics of single auditory neurons are presented for the first time. The transfer characteristics of receptor cells and ascending ventral-cord neurons are evaluated with respect to a special test signal ("modulation signal"). The test signal determines the temporal course of the actual sound pressure of the stimulus. The use of the white-noise method has the advantage of applying only one particular test signal instead of a very large number of stimuli with varying amplitude and duration. The computational burden is within a reasonable range. The receptor cells in general show a good linear and quadratic coupling between the test signal and their responses whereas the ascending ventral-cord neurons normally do not. The responses of the receptors in contrast to the central auditory neurons depend only on the difference between the actual threshold and the sound-pressure level of the stimulus and not on the carrier frequency of the stimulus signal.

Introduction

The auditory system of the migratory locust *Locusta migratoria* has been investigated in detail by electrophysiological and neuroanatomical methods. Single neuron recordings and staining techniques have led to a very detailed description of the function and structure of most of the neurons within the auditory pathway (Adam, 1969; Michelsen, 1971; Kalmring et al., 1972; Rehbein et al., 1974; Kalmring, 1975). For these studies a large number of various kinds of stimuli were neccessary to determine the actual properties of neuronal information processing.

The most general way to describe a system, however, is to evaluate its transfer functions, that is, to be able to predict its response to any arbitrary input signal. This paper takes advantage of the white-noise method – i.e. special application of system theory – to obtain the signal transmission characteristics of a given system – even if it is nonlinear – by using only one particular input signal (Marmarelis and Marmarelis, 1978). Furthermore, model responses due to any input signal can be computed by forming the corresponding folding integral with the Wiener kernels representing the transfer characteristics of the system.

For this purpose the dependence of a neuron's reaction on the course of the sound-pressure level of an appropriately adapted stimulus signal is investigated with respect to the domain of time and frequency. The investigated neurons are various receptor cells and ventral-cord neurons ascending to the supraesophageal ganglion (SEG).

Material and Methods

1. White-Noise Method

Volterra showed that for any given system that is analytic, nonlinear, time invariant, and has finite memory, the input ($x(t)$)-output ($y(t)$) relationship can be described completely by a functional series as:

$$y(t)=\sum_{n=0}^{\infty} F_n\{x(t)\} \tag{1}$$

with $x(t)$: stimulus; $y(t)$: response.

The first terms of this "Volterra series" (1) are:

$$\begin{aligned} y(t)=k_0&+\int_{-\infty}^{\infty} k_1(\tau)\cdot x(t-\tau)d\tau\\ &+\iint_{-\infty}^{\infty} k_2(\tau_1,\tau_2)\cdot x(t-\tau_1)\cdot x(t-\tau_2)d\tau_1 d\tau_2\\ &+\iiint_{-\infty}^{\infty} k_3(\tau_1,\tau_2,\tau_3)\ldots, \end{aligned} \tag{2}$$

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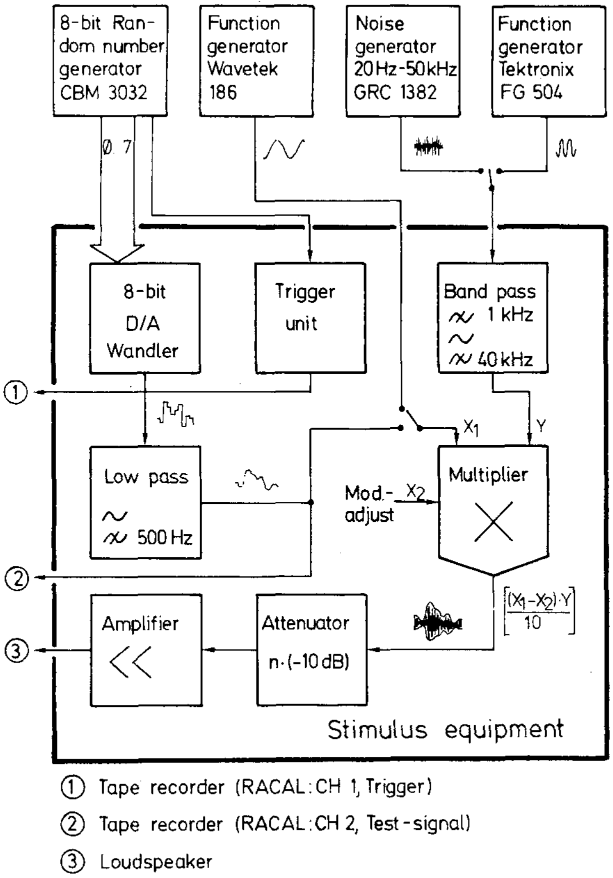

Fig. 1. Scheme of the stimulus equipment for generating the test and stimulus signal

where k_n are the so called kernels of the system which completely can be described if all of them are known. The Volterra series converges very poorly and in practice it is impossible to determine the kernels of the system.

Wiener (1958) orthogonalized the terms of the Volterra series under the condition that the input signal $x(t)$ is Gaussian white-noise (GWN). Now the input-output relationship can be described as:

$$y(t)=\sum_{n=0}^{\infty} G_n[h_n, x(t)] \tag{3}$$

$x(t)$: the input signal is "Gaussian white-noise" (GWN), h_n: n^{th} order Wiener kernel satisfying the condition of orthogonality:

$$E[\![G_n * G_k]\!]=0 \quad \text{for} \quad n \neq k. \tag{4}$$

The first three functionals of the Wiener series are:

$$G_0[h_0, x(t)]=h_0,$$

$$G_1[h_1, x(t)]=\int_0^{\infty} h_1(\tau)\cdot x(t-\tau)d\tau,$$

$$G_2[h_2, x(t)]=\iint_0^{\infty} h_2(\tau_1,\tau_2)\cdot x(t-\tau_1)\cdot x(t-\tau_2)d\tau_1 d\tau_2$$

$$-P\int_0^{\infty} h_2(\tau_1,\tau_1)d\tau_1$$

with h_0: mean, h_1: impulse response of a linear (LTI-) system, $P=\Phi_{xx}(f)$: Power of the GWN-signal equivalent to the autocorrelation function of the input $x(t)$.

If we know all the kernels of a system we can describe the system entirely. Because of the orthogonality of the G-functionals the number of the required kernels depends only on the order of the system's nonlinearities. Lee and Schetzen (1965) showed that multiplication of the Wiener series by homogenious functionals of increasing order according to

$$x(t-\mu_1)\cdot x(t-\mu_2)\cdot\ldots\cdot x(t-\mu_n)$$

generally results in:

$$h_n(\tau_1,\ldots,\tau_n)=(1/n!P^n)\cdot E\left[\!\!\left[\left(y(t)-\sum_{k=0}^{n-1} G_k[h_k, x(t)]\right)\cdot x(t-\tau_1)\cdot\ldots\cdot x(t-\tau_n)\right]\!\!\right] \tag{5}$$

for the Wiener kernel of the n^{th} order.

The use of GWN as a test signal for the analysis of the properties of a given system is illustrated by the following idea: Any possible function of time can be approximated – within a given accuracy – by a section of this GWN signal, which represents a random function of time, provided the stimulation has a sufficient duration. Thus, the system is tested by all possible functions of time and frequency, over which the GWN-signal has a flat spectrum.

2. *Stimulus Generation*

The reactions of the acoustic neurons with regard to the actual sound pressure will be analysed. Hence, a stimulus which is represented by the course of sound pressure corresponding to the temporal variation of a GWN-signal has to be chosen. The most simple way to do this is to modulate a carrier signal situated within the locust's range of hearing with a low-frequency band-limited GWN which is not extended to this range. Thus, the modulation signal represents the input (test signal) demanded by the white-noise method. The band-limitation upper corner frequency was 500 Hz covering the total system's bandwidth (below 200 Hz) without extending to the locust's range of hearing (> 1 kHz, Fig. 2b).

The test signal was generated by a microprocessor system as a temporal sequence of 8-bit (pseudo-)random numbers with a Gaussian amplitude distribution according to a procedure described in Eckhorn and Pöpel (1979). The duration of the sequence was 2.02 s. It was repeated continuously and was applied in all experiments in the same way.

The final stimulus signal was generated by the equipment illustrated schematically in Fig. 1. The temporal sequence of 8-bit random numbers was converted into an analog signal and then, after low-pass filtering (frequency limit 500 Hz, cf. Fig.8a), represented the desired GWN-test signal. Either band-limited GWN (1 kHz...40 kHz; General Radio Comany, Mod. 1382) or sinusoidal pure tones (Function Generator, Tektronix FG 504) were used as carrier signals. The modulation was performed by a multiplier, which was additionally fed with a DC-offset (input X_2), enabling a modulation range of at least 95 %. Thus, a dynamic range of about 26 dB can be achieved which is within the dynamic range of the receptor cells. The stimulus signal generated in this way fed an end-amplifier (attenuation in 10 dB-steps), the output of which was passed to a HF-loudspeaker (Audax TW 8 special) for stimulation.

3. *Data Registration and Evaluation*

The neuronal response $y(t)$ is considered as a temporal function of impulse probability's density (IPD) which was approximated by computing the relative impulse frequency in its course of time. The spike-trains of one experiment (for 20 identical stimulus periods) were averaged and filtered digitally by a "von Hann window" with to a frequency limit of 100 Hz (Hamming, 1977). This procedure resulted in a quasi-continuous course of response from which the

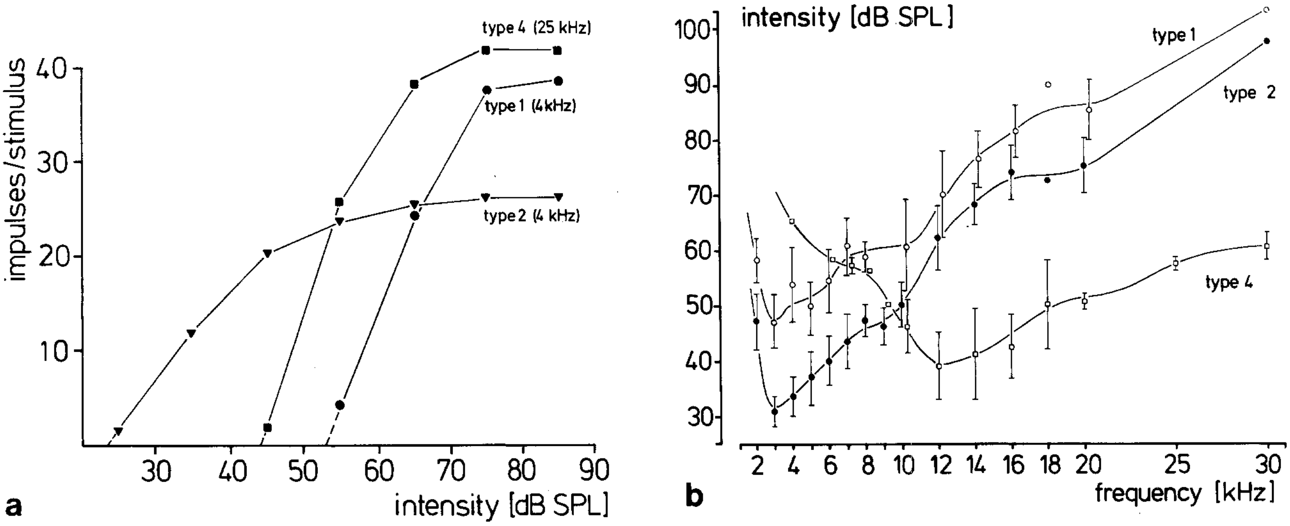

Fig. 2. **a** Intensity-characteristics of various receptor cell types: Sinusoidal stimulus (4 kHz: type 1 and 2; 25 kHz: type 4), duration 100 ms, repetition rate 2/s (modified from Römer, 1976). **b** Auditory threshold curves of single receptor neurons. Standard sinusoidal stimuli: duration 20 ms, repetition rate 2/s (modified from Petersen et al., 1982)

Wiener kernels up to the second order (h_0, h_1, h_2) as well as the corresponding model responses (linear and quadratic) were computed (Sippel, 1982). Any kernel of higher order is not considered because of an exponential increase in calculation expense with the order n of the desired kernel. Using only the first n Wiener kernels to describe the system, the best n^{th} order description is also obtained (in the sense of a least mean square error MSE). Therefore a stringent test of the goodness of our description (model) is to compare the computed response to the GWN test signal with the actual response of the system. For that we evaluate the mean-square deviation of the model response from the actual response dividing it by the mean-square deviation of the actual response from h_0 which is set to 100%. In this way we get the MSE in per cent as a measure of the goodness of fit of the computed model.

4. *Preparation and Recording Techniques*

Preparation and recording techniques are described in detail elsewhere (Kalmring et al., 1978; Petersen et al., 1982). The system's response, i.e. the recorded spike-trains, and the GWN-test signal are stored on tape recorder (Racal 4 D Store). All calculations are done by a computer (Hewlett Packard HP 1000).

Results

1. *Sinusoidal Modulated Stimulation*

The acoustic receptor neurons of *Locusta migratoria* are classified in 4 groups according to their functional and structural properties (Michelsen, 1971; Römer, 1976; Michel and Petersen, 1982; Petersen et al., 1982). The threshold curves and intensity-characteristics relations of three of these groups are shown in Fig. 2. Standard stimulation (cf. legend) was applied.

Figure 3 illustrates the sinusoidal test signal (Fig. 3a), the corresponding spike-trains and the unfiltered impulse frequency (Fig. 3b and c) of a type 2 receptor cell. The modulation frequency was 10 Hz and the mean intensity was 35 dB SPL. The carrier frequency was tuned to the "best frequency" of the type 2 cell, which is about 4 kHz. The system's response relation on stimulus-intensities (e.g. Fig. 3d, 35 dB SPL) is achieved by digital hanning of the impulse-frequency distribution (e.g. Fig. 3c). Increasing intensity (Fig. 3e, 45 dB SPL) results in higher amplitudes as well as in better synchronicity of the responses. Further increase to 55 dB SPL, however, causes response decrease below the value for 35 dB (Fig. 3f). With increasing intensities, however, latency decreases monotonically. In contrast with standard-stimulation there is a linear increase of impulse frequency within this range of intensities (Fig. 2a). The power spectra (Fig. 4) show that this response reduction is accompanied by an increase of the share of higher harmonics. Thus, at this level the system reacts extremely non-linearly; a further analysis could not be done because of the high computational burden. Near threshold level (35 dB and 45 dB SPL), on the other hand, a second-order model (G_0, G_1, G_2) would sufficiently describe the system's properties. This receptor type responds in a phase-locked manner up to 100 Hz with variation of the modulation frequency. No significant frequency dependence of the IPD is recognizable (Fig. 5). Therefore, the distribution of the power components remains constant and depends only on the stimulus intensity. If a broad-band GWN (1 kHz...40 kHz) instead of the characteristic-frequency (4 kHz) as a carrier signal is chosen, the power distribution shows considerably less harmonics. Hence, the most appropriate way for applying the white-noise method is to use stimuli near the threshold intensity range and possessing GWN as the carrier frequency.

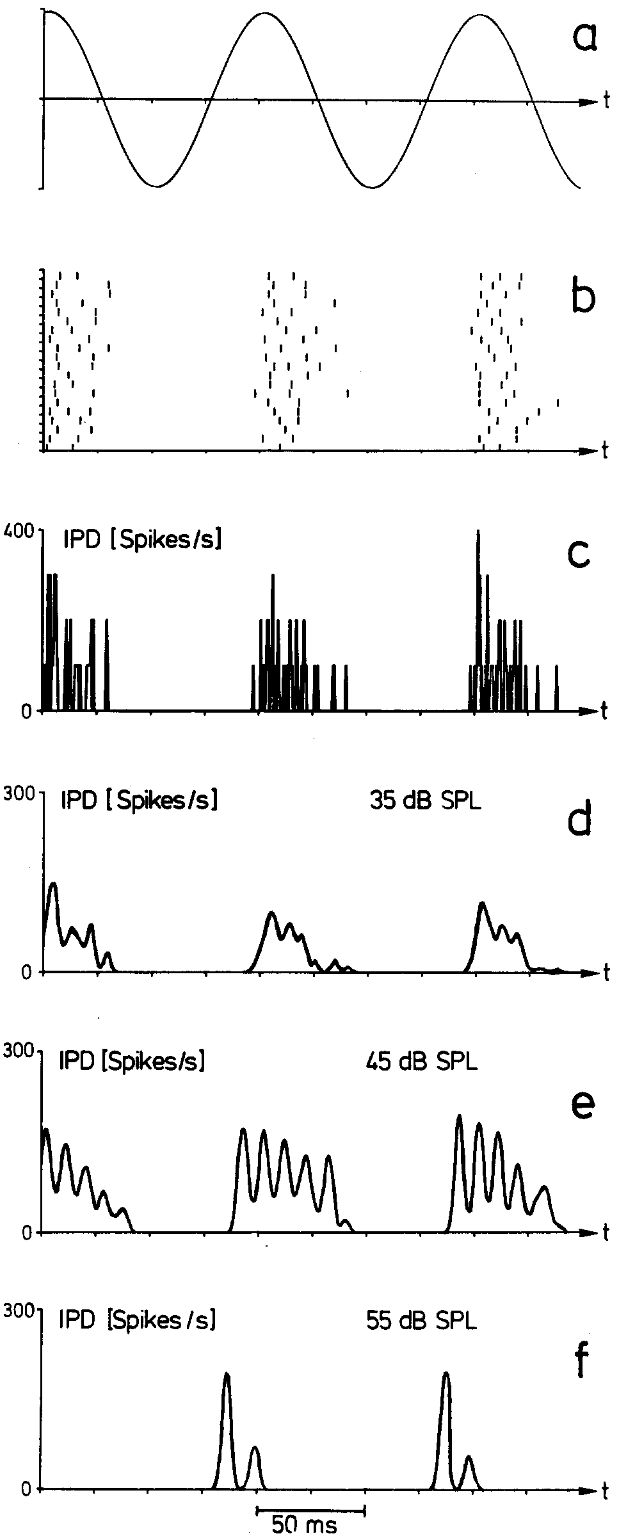

Fig. 3a–f. Response of a type 2 receptor neuron due to sinusoidal modulated stimulus signals of various intensities. Modulation frequency 10 Hz, carrier frequency 4 kHz. **a** Modulation signal, **b** spike-trains for 20 identical stimulus periods, 35 dB SPL, **c** impulse probability's density (IPD), not filtered, 35 dB SPL, **d** IPD, filtered by digital hanning, i.e. the system's response, 35 dB SPL, **e** system's response, 45 dB SPL, **f** system's response, 55 dB SPL

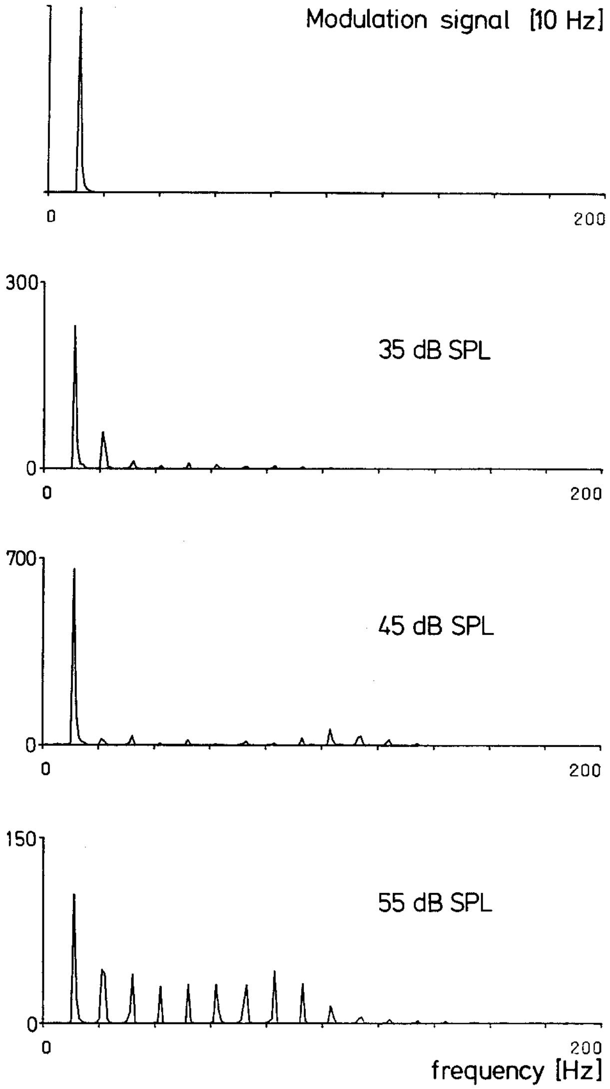

Fig. 4. Power spectra of the system's responses shown in Fig. 3

2. *White-Noise Method*

2.1. Receptor Neurons. In the same way described in Part 1, the system's response is calculated by averaging and low-pass filtering the spike-trains of a single cell recorded in response to 20 identical stimulus periods (Fig. 6a–d). The system's response is then used to compute the Wiener kernels and the corresponding model responses. The results of the linear (G_0, G_1) and the non-linear (G_0, G_1, G_2) analysis are shown in Fig. 6e–g. The recorded neuron is of type 1. The carrier signal is GWN and the sound intensity is 65 dB SPL, i.e. about 10–20 dB above threshold. The computed linear model (Fig. 6e) already shows a satisfactory conformity to the system response (MSE = 47%). The quadratic model (Fig. 6g) gives an improvement up to a MSE of 33%. The kernels used for computing the model responses are shown in Fig. 6d ($h_0 = 37$ spikes/s;

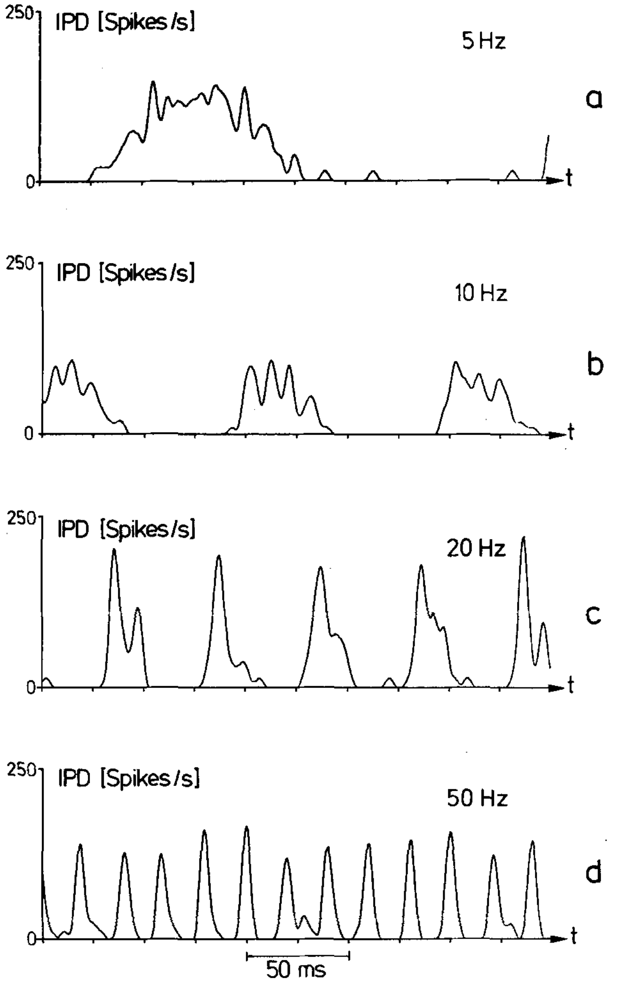

Fig. 5a–d. System's response of a type 2 receptor neuron due to stimuli of various modulation frequencies. Carrier frequency 4 kHz, 44 dB SPL. Modulation frequency **a** 5 Hz, **b** 10 Hz, **c** 20 Hz, **d** 50 Hz

indicated at the ordinate) and in Fig. 7a and b. The course of h_1 (representing the linear transfer function) exhibits a strong positive maximum at about 13 ms corresponding to low-pass transfer characteristics, and a subsequent smaller negative maximum related to a slight band-pass behaviour (Fig. 7a). The time of 13 ms represents latency, including 4 ms delay caused by the propagation time from the loudspeaker to the animal (2 ms) and by the lag of the data processing equipment (2 ms). The width of these peaks are related to the frequency limits of the intrinsic filters. The kernel h_2 depends on the two time variables τ_1 and τ_2. The plotting of the kernel h_2 results in a three-dimensional field as shown in Fig. 7b. The corresponding power spectrum of the test signal, the system's response and the model responses are illustrated in Fig. 8. Here also linear low-pass properties can be recognized reflecting the fundamentally tonic reaction mode of the receptor neurons. In addition slight band-pass properties exist.

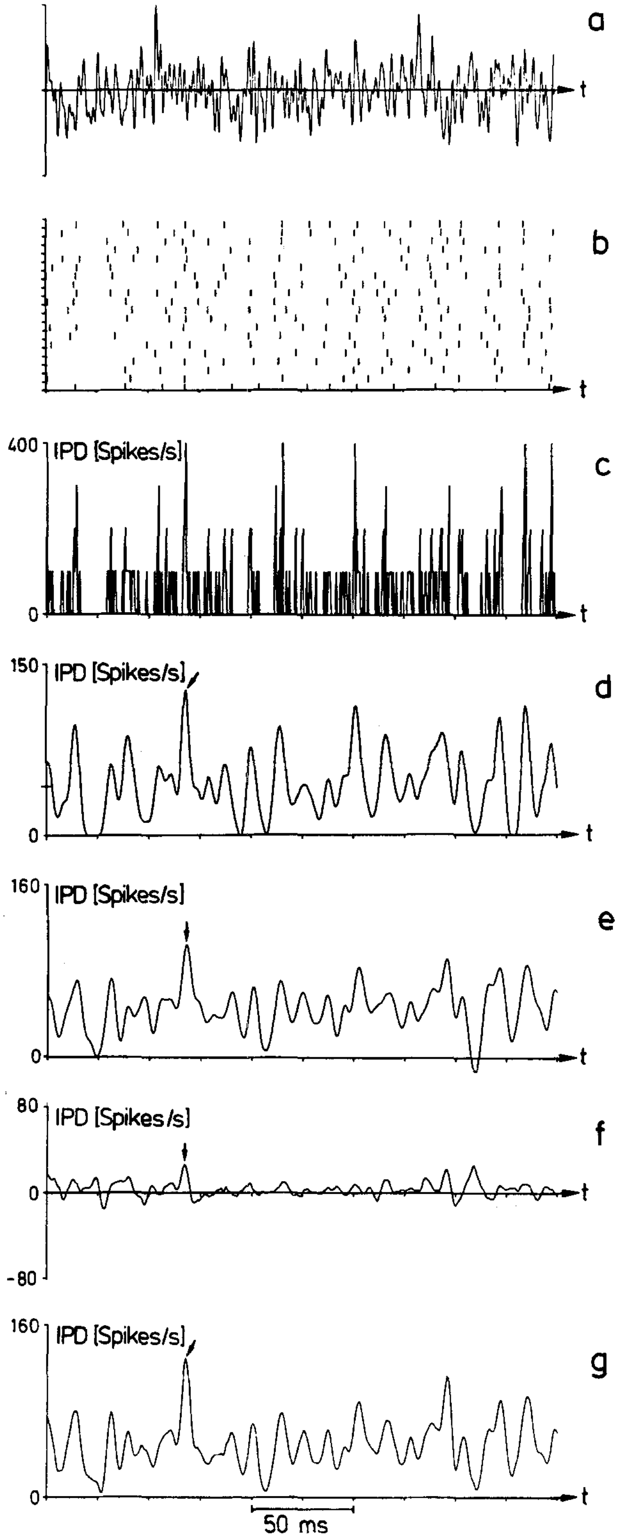

Fig. 6a–g. Response of a type 1 receptor neuron due to a GWN-modulated stimulus signal and its calculated model responses. Test signal GWN, carrier signal WN, 65 dB SPL. **a** Temporal course of the test signal (section 250 ms), **b** spike-trains for 20 identical stimulus periods, **c** IPD, not filtered, **d** system's response, **e** linear model response (G_0, G_1), **f** quadratic model response (G_2), **g** non-linear model response (G_0, G_1, G_2)

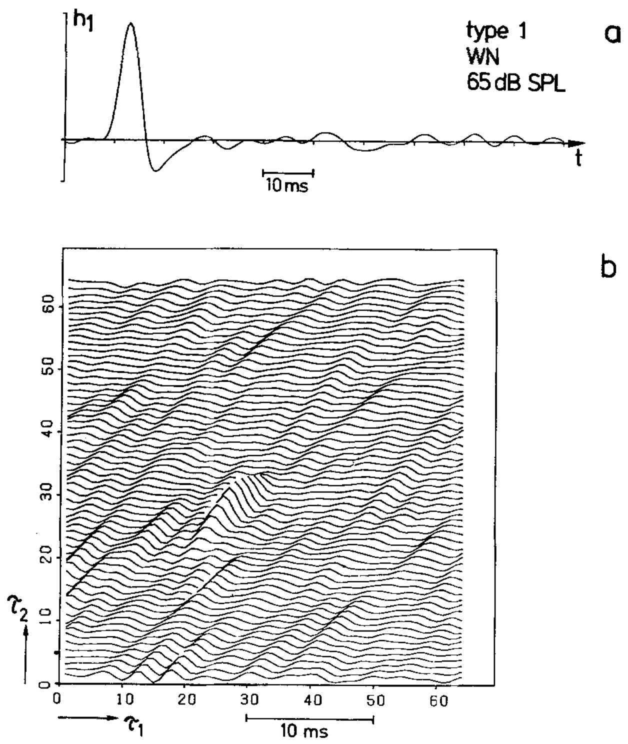

Fig. 7a and b. Wiener kernels of a type 1 neuron's response. **a** Wiener kernel h_1, **b** Wiener kernel h_2

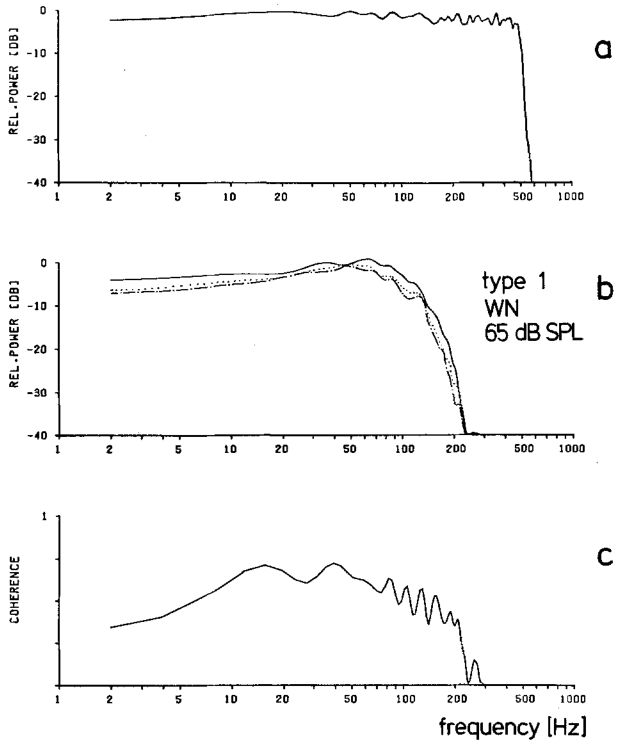

Fig. 8. a Power spectrum of the test signal. **b** Power spectra of a type 1 neuron's response. ——— system's response, —·—·— linear model (G_0, G_1), ------ non-linear model (G_0, G_1, G_2), **c** Coherence function (system's response/test signal)

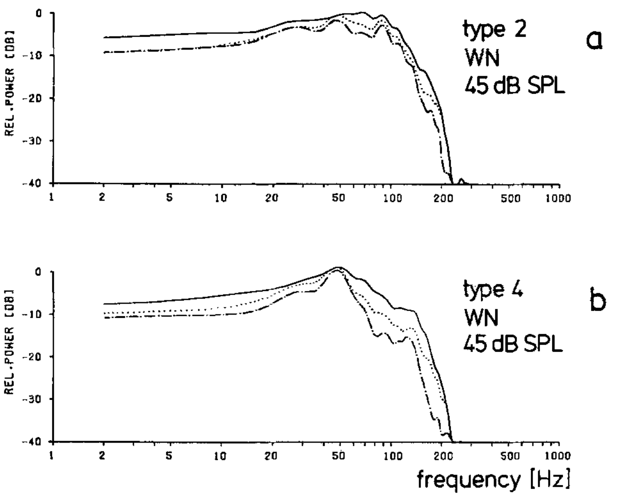

Fig. 9a and b. Power spectra of a type 2 **a** and a type 4 **b** receptor neuron's responses. Carrier signal WN, 45 dB SPL

Obviously also the response properties of this neuron in the frequency range can be sufficiently approximated by the computed models. The model spectra show the smallest deviation in the range between 15 and 50 Hz. The neuron reacts more or less regularly up to 100 Hz, slightly prefering modulation frequencies between 30 and 80 Hz. The strong decrease within the power spectrum above 100 Hz is mainly due to the digital low-pass filtering of the data.

It is possible to show whether a system is free of noise and/or non-linear by drawing up the coherence function $k(f)$ (Fig. 8c). This represents a measure of the correlation between the system's response and the input signal, where $k(f) = 1$ means total coherence and absence of noise. For the response shown in Fig. 8b $k(f)$ also differs from 1 for the frequency range around 50 Hz, where even the linear model corresponds almost completely with the response spectrum, i.e. the system here has to be linear. However, the system as a whole, is not only non-linear but also – as expected – not free from noise.

In Fig. 9a and b the power spectra for receptor cells of the types 2 and 4 are shown. In both cases the carrier signal is GWN. The stimulus intensity is 45 dB SPL, i.e. about 10–20 dB above the actual thresholds. The type 2 spectrum is very similar to that of type 1 (response maximum between 50 and 70 Hz), whereas type 4 exhibits more non-linear characteristics. A slight increase in the spectral power density is seen at 40–60 Hz. A subsequent depression above 60 Hz is particularly striking for the linear model.

In all cases the response behaviour does not basically depend on the kind of carrier signal.

The possibility that the spectra maxima about 50 Hz could be due to influences of the power supply

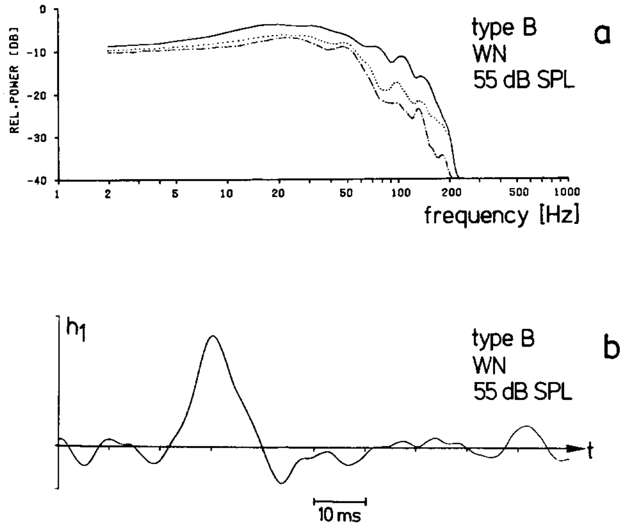

Fig. 10a and b. Power spectrum **a** and Wiener kernel h_1 **b** of a B-neuron's response. Carrier signal WN, 55 dB SPL

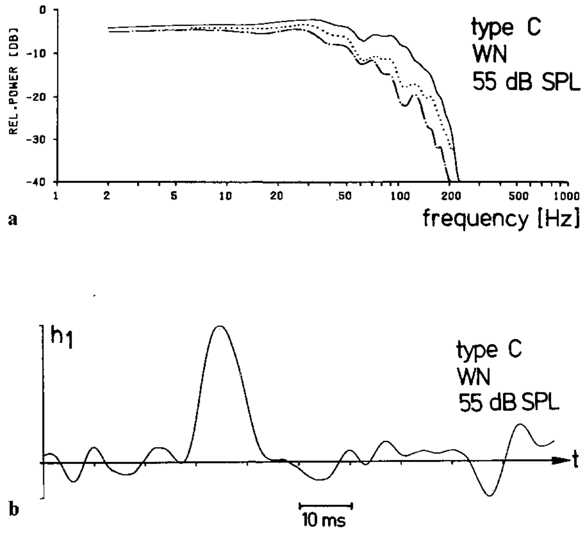

Fig. 11a and b. Power spectrum **a** and Wiener kernel h_1 **b** of a C-neuron's response. Carrier signal WN, 55 dB SPL

can be excluded since the tape recordings were free of this distortion.

2.2. Ventral-Cord Neurons. In investigating these neurons GWN as well as various sinusoidal carrier stimuli were applied. The latter, however, produced non-linearities of such high order, that the non-linear discription (h_0, h_1, h_2) led to no satisfying results. In contrast to the receptor cells the ventral-cord neurons react differently with regard to the actual carrier signal. For further investigations only GWN was used. The power spectra and kernels of the first order h_1 of a B-neuron and a C-neuron, respectively are shown in Figs. 10 and 11 [classification after Popov (1967) and Kalmring (1975)]. Mainly low-pass characteristics can be seen and no band-pass is visible. In contrast to the receptor cells the depression of the power spectra sets on at lower frequencies (about 50 Hz). The mean spike-frequencies (h_0) are very low with as a rule 20–30 spikes/s (receptor cells: $h_0 = 30$ to 60 spikes/s).

The central neurons often react in a similar way with test signals of different sound intensities, i.e. here the response does not depend on the absolute sound pressure anymore but only on the relative values with regard to the actual (mean) sound-pressure level (especially valid for the C-neurons). Thus, these (C-) neurons must have inputs from several receptor types in order to be able to transmit the relative course of the test signal within such an extended range.

Other ventral-cord neurons [there are about 14 acoustic neurons at each body side, as classified by Kalmring (1975)] were recorded. However, they exhibited a strong habituation to the actual (constant) mean sound-pressure level after stimulus onset. For example, the spike frequency of a G_1-neuron, decreased within less than 1 s from an initial 30 to 40 spikes/s to less than 1 spike/s. Thus, a white-noise analysis with regard to the chosen stimulus was not possible. Sinusoidal modulations of various frequencies, intensities and carrier signals led to similar results. Obviously, these neurons habituate and react only to a relatively rapid increase of the constant mean sound-pressure level with a short spike-burst. Hence, they exhibit strongly differentiate the dynamic components of the stimulus.

Discussion

The central nervous processing of the investigated ventral-cord neurons (C-, partly B-type neurons) generally results in an increase in the operating range in comparison to that of the receptor cells, with reference to the intensity range of the stimulus signal (cf. Kalmring, 1975). The (linear and quadratic) coupling of the test signal and system response, however, decreases and often almost entirely vanishes. This is caused by non-linearities of higher order and/or a strong influence of internal signals not being correlated to the stimulus. In contrast to the receptor cells, the use of GWN carrier signals shows a striking difference from that of sinusoidal signals. In the latter case we found only a very small (linear) correlation between test signal and system response.

The results we have to deal with suggest that the central (C-) neurons are able to transmit the course of the test signal (linearly and quadratically) only if they receive inputs from several receptor types via intercalated interneurons.

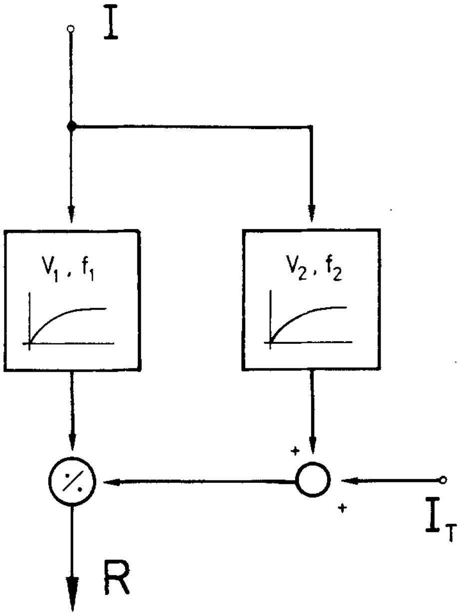

Fig. 12. Receptor model. Explained in text (modified from van de Grind, 1973)

In the present analysis the temporal fluctuations (e.g. internal noise) of the system's response behaviour are averaged to zero and thus, as well as habituation and adaptation processes, are not considered. The biological system, however, has to be able to handle such fluctuations. This is probably done by parallel, partly manifolded, signal transmission and processing. Furthermore, the central neurons are tuned to the special (also extremely non-linear and non-steady) transmission properties of the preceding receptor and inter neurons. Thus, the locust is able to react "on-line" to the various acoustic signals from the environment in an adequate way.

An additional problem is that of the biological relevance of the stimulus signal being used which, indeed, is a continuous, relatively narrow or broadband noise with constant mean sound-pressure level. The test and stimulus signal, respectively, is transmitted more or less completely in the form of corresponding spike-trains by the receptor cells. However, regarding the central neuronal level several neurons don't show a significant reaction at all (as shown in the case of the G_1-neuron). But the central neurons are able to transmit temporal patterns of series of impulse signals (e.g. the stridulation songs) very well. Therefore our stimulus signal was not quite as suitable for those experiments as for the receptor cells. It could well be interpreted by locusts in the biotope as a constantly present background noise, which doesn't have a considerabel importance for the animal.

The response characteristics of the investigated receptor neurons, e.g. type 1 (Fig. 8b), seems to exhibit a more general feature found also in receptors of other sensory systems. Van de Grind (1973) proposed a retinal receptor model consisting of linear filters representing photochemical and chemico-electrical processes in the receptor. Reichardt (1961) assumed a similar model to account for the light reaction of *Phycomyces.* In an analogy to these the response characteristics of the acoustic receptor neurons of *Locusta migratoria* might be described by a model illustrated in Fig. 12. F_1 and F_2 (frequency limit f_1, f_2, respectively) are linear low-pass filters satisfying the condition $f_2 < f_1$. I_T is the receptor's threshold intensity at a given level of adaptation. The frequency transmission property of this system is characterised by a low-pass behaviour superimposed by a band-pass, the size of which depends on the relation of f_1 and f_2 as well as the gains (V_1, V_2, respectively) of the filter elements. The static relationship between the suprathreshold intensity I of a steady sound stimulus and the receptor's response R is non-linear and is given by

$$R = V_1 I/(I_T + V_2 I)\,. \tag{6}$$

I_T determines the size of the slope R in the near threshold range and represents the (approximated linear) dynamic range of a given receptor cell. Equation (6) accounts satisfactorily for the receptor's reaction as shown in Fig. 2a. The saturation range is defined by $R \approx V_1/V_2$. In the dynamic case treated in Results Sect. 1, either V_1 or V_2 must depend on the sound intensity I causing a decrease of R with increasing I at high suprathreshold levels (cf. Fig. 3). What this dependence is quantitatively and which structural and functional receptor elements correspond to the model components is, however, still unknown.

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