

PREDICTION OF LINEAR AND NON-LINEAR RESPONSES OF MGB NEURONS BY SYSTEM IDENTIFICATION METHODS

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In sensory physiology, various System Identification methods are implemented to formalize stimulus-response relationships. We applied the Volterra approach for characterizing input-output relationships of cells in the medial geniculate body (MGB) of an awake squirrel monkey. Intraspecific communication calls comprised the inputs and the corresponding cellular evoked responses—the outputs. A set of vocalization was used to calculate the kernels of the transformation, and these kernels subserved to predict the responses of the cell to a different set of vocalizations. It was found that it is possible to predict the response (PSTH) of MGB cells to natural vocalizations, based on envelopes of the spectral components of the vocalization. Some of the responses could be predicted by assuming a linear transformation function, whereas other responses could be predicted by non-linear (second order) kernels. These two modes of transformation, which are also reflected by a distinct spatial distribution of the linear *vis-à-vis* non-linear responding cells, apparently represent a new revelation of parallel processing of auditory information.

1. Introduction. Characterization and full description of stimulus-response relations in the central nervous system is a major goal in experimental neurobiology. However, due to the complexity and apparent nonlinearity of these relationships, it is practically impossible, in many cases, to achieve this goal by simply employing visual inspection, or even fundamental semi-quantitative techniques, as is often done. We confronted this problem while attempting to obtain some insight into the role of the medial geniculate body (MGB) of an awake squirrel monkey, in the processing of auditory signals. Typical of the higher levels of the auditory pathway, many of the MGB cells reveal highly complex response patterns to various auditory stimuli, and particularly to intraspecific communication sounds which are spectrally and temporally very complex (Symmes *et al.*, 1980; Allon *et al.*, 1981; Allon and Yeshurun, 1985). Failing, in most cases, to relate response properties to stimuli characteristics by employing conventional methods, we tried System Identification methods, which we applied to a sample of 41 cells. The approach which we adopted and modified was the Volterra approach (Hung and Stark, 1977; Marmarelis and Marmarelis, 1978; Yeshurun *et al.*, 1985).

The functional identification of a system is carried out by obtaining the transfer function which relates the output of a system to its input. If that

function can be defined, then the operation of the system is also defined and predictable. This approach is usually applied when the internal structure of the system is not known and is considered as a "block box" (Allon *et al.*, 1981). The inputs are applied to the auditory system, and the output is recorded from single cells in the MGB. Thus, the system identified by us is actually a subset of the auditory pathway. It consists of a network with boundaries ranging from the peripheral aspect of this pathway on the one extreme, to a single MGB cell on the other extreme. Many aspects of the inner structure of the system are not well known, despite the fact that ample information is available, regarding its cytoarchitecture and the connectivity pattern of the MGB with the other components of the auditory system.

In the following, we describe the system's input and output, the formal model, and the results obtained by applying it to responses of MGB cells.

2. The Formal Model. Most identification methods which are applied to neurobiological systems use white Gaussian noise as the stimulus (Hung and Stark, 1977; Eggermont *et al.*, 1983), thus using the Wiener-Volterra approach (Wiener, 1958). White noise, though undoubtedly superior to other stimuli from a theoretical point of view (Wiener, 1958), might not necessarily be the optimal stimulus from a biological point of view. Indeed, several physiological studies demonstrated that complex sounds, and especially calls which possess a biological communicative value, are more effective, compared with conventional auditory stimuli, including white noise, in eliciting responses at the upper levels of the auditory system (Capranica, 1972; Newman and Wollberg, 1973; Suga, 1978; Ploog, 1981). The inputs which we employed, therefore, were tape-recorded, intraspecific communication calls (Winter *et al.*, 1966) presented to the monkey during the physiological experiments, in a normal and a reversed version (reversed vocalizations have the same spectral components as normal vocalizations, but are not assumed to carry "semantic" information). The frequency range where most of the vocalizations' energy is concentrated is between 0.5 and 20 kHz, and the techniques of recording and playback of the vocalizations are described elsewhere (Yeshurun *et al.*, 1985). The auditory input can generally be represented in terms of acoustic energy function $P(t)$. However, if a reasonable time resolution is required, then a digitized vocalization would consist of some ten thousands of values. Instead, the input is represented by its spectral components, each component having its temporal energy distribution. Throughout the identification procedure these calls were represented by the digitally filtered spectral components, as 1/3 octave resolution. The use of spectral components of the calls rather than the calls themselves, rests also on the assumption that the operation of the auditory nerve can be roughly approximated by a bank of overlapping filters (Evans, 1977). Part of the system's activity, in our model, can therefore be considered

explicit rather than implicit, thus reducing the complexity of the identified system. By "removing" the first phase of the processing from the black box, the identified system is receiving a multi channel input, namely, is a multi-input system.

The outputs of the system were the responses of single MGB cells evoked by the calls and by their corresponding reversed versions, represented by smoothed Peri-Stimulus Time Histograms (PSTHs). The PSTH is obtained by presenting the vocalizations for 15 consecutive times (Yeshurun *et al.*, 1985), using bin duration of 3 ms.

We identify, thus, a multi-input and single output system (Marmarelis and Naka, 1974), which is schematically illustrated in Fig. 1. The model can be mathematically described as follows.

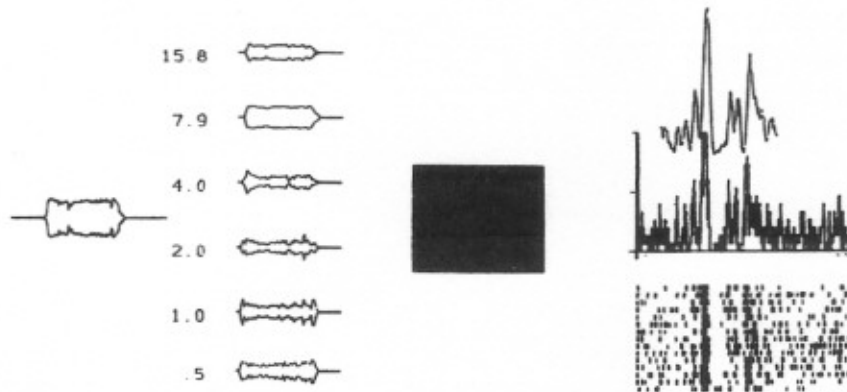


Figure 1. A scheme of the system. The original auditory input (extreme left) is decomposed into its spectral components (left). Each component is represented by its amplitude envelope. This is a rough approximation of the spectral decomposition that is carried out in the first stage of the auditory system, such that the identified system is assumed to receive many band limited channels. This comprises the multi-input aspect of the system. In this analysis we used 1/3 octave resolution, resulting in 18 inputs. For the illustration, only 6 inputs, obtained by 1 octave resolution, are depicted. The centre frequency of the spectral components are denoted to their left. The inputs enter the system (denoted by a black box), which transforms them to the output. The output (right) consists of the recorded responses to 15 consecutive identical stimuli; represented by a dot raster display (bottom), transformed into a regular PSTH (3 ms bin duration, middle panel) and a smoothed PSTH (by a moving average of 3 ms width, top panel).

The system we analyse is a multi-input and single output one. The inputs are the temporal energy distributions of m spectral components, denoted by $x_1(t)$ to $x_m(t)$, and the output is the smoothed PSTH denoted by $Y(t)$. In this study $m = 18$, determined by assuming 1/3 octave resolution over the effective range

(0 to 20 kHz) of the vocalizations. Assuming the validity of the Volterra representation for this system, its functional aspect can be described as:

$$Y(t) = F\{x_1(t), \dots, x_m(t)\} = \sum_{i=1}^{\infty} Y_i(t),$$

where:

$$Y_i(t) = \sum_{j_1=1}^m \dots \sum_{j_i=1}^m \int_0^M \dots \int_0^M H_{j_1 \dots j_i}(\tau_1, \dots, \tau_i) \prod_{p=1}^{j_i} x_p(t - \tau_p) d\tau_1 \dots d\tau_i.$$

M denotes the length of the system (10 ms in this study). An approximation up to the second order of the Volterra representation is:

$$Y(t) = Y_l + Y_q,$$

where:

$$Y_l = \sum_{r=1}^m \int_0^M H_r(\tau) x_r(t - \tau) d\tau,$$

$$Y_q = \sum_{r=1}^m \sum_{s=1}^m \int_0^M \int_0^M H_{rs}(\tau_1, \tau_2) x_r(t - \tau_1) x_s(t - \tau_2) d\tau_1 d\tau_2.$$

Here $H_r(\tau)$ is the linear kernel associated with the input $x_r(t)$, and $H_{rs}(\tau_1, \tau_2)$ is the quadratic kernel associated with inputs $x_r(t)$ and $x_s(t)$.

In order to compute the kernels, each one is regarded as a series in:

$$\{Q_i(t) = e^{-t} L_{i+1}(t)_{i=0}^{\infty}\},$$

where $L_i(t)$ are the Laguerre polynomials. In that case each kernel is approximated by a finite number of terms in its expansion:

$$H_{rs}(\tau_1, \tau_2) = \sum_1^k \sum_1^k \alpha_{ij}^{rs} Q_i(\tau_1) Q_j(\tau_2), \quad H_r(\tau) = \sum_1^k \alpha_i^r Q_i(\tau).$$

Each vocalization-response pair can be described, after discretization, by a set of equations, and several such pairs comprises an overdetermined set of equations in the vector of α_i and α_{ij} (Watanabe *et al.*, 1975). The solution of this set leads to the calculation of the system's transfer functions, which consists in our model of the first and second order kernels.

Obviously, it cannot be theoretically proved that the system is exhaustively described by a second order model. The only way such an approximation can be justified should bear on the ability of the model to predict cells' responses.

Since the kernels describe completely the transformation of the input functions into the output functions, the process of identification is basically completed by their evaluation. An immediate outcome of this procedure is the ability to simulate the operation of the system. Namely, having computed the kernels, one should be able to predict the responses of an MGB cell to any given auditory stimulus. Moreover, on the basis of the calculated kernels, and by analysing the predicted responses, one would expect to obtain some ideas regarding the *modus operandi* of the system. Indeed, several of these expectations were achieved (Yeshurun *et al.*, 1985, 1987). In the following we describe results and conclusions concerning linear and non-linear (quadratic) processes in the MGB.

3. Prediction of Responses by Linear and Quadratic Kernels. The Volterra representation of a system is formally valid if some conditions (e.g. causality and Frechet continuity) are fulfilled (Hung and Stark, 1977). In general, it is almost impossible to formally prove that a biological system does not violate any of these conditions. However, a model can be considered useful if it predicts responses of the system. This is the approach taken in this study: the kernels are computed for each cell by a set of input-output pairs, and then are used to predict the response of this cell to a different set of inputs. This is one of the basic results of this study: it is possible to predict responses of single cells in the higher parts of the auditory system (the MGB) to natural vocalization, based on its responses to other vocalizations.

It can generally be stated that a neural network is, by and large, a non-linear system since some of its basic features are non-linear. However, linearity can still be detected in a limited subset of the response space, if and when it represents either an actual linear process or a local linear behaviour of a non-linear system. The auditory system reveals highly non-linear features, of which the various forms of two tone combinations are only one illustration (Goldstein, 1967; Pfeifer and Kim, 1973). Discriminating linear from non-linear systems is interesting and important from both the experimental and the theoretical points of view: the study of linear systems is much more developed and quantitatively formalized; and this distinction is highly related to the processing principles of the system under consideration. Such a distinction can be obtained by applying Volterra models to the system: the identification procedure can be carried out for several variants of the mathematical model, with every variant being characterized as linear (first order kernels only) or non-linear (higher order kernels in general, and quadratic kernels in this study). The quality of the predicted responses, as defined by the MSE distance

between the actual response and the predicted one, can be utilized for evaluating the validity of the representation.

Representative illustrations of the predictions we made according to this procedure are depicted in Fig. 2. (A quantitative evaluation of the predictions can be found in Yeshurun *et al.* (1985, 1987).) It can be seen that some of the

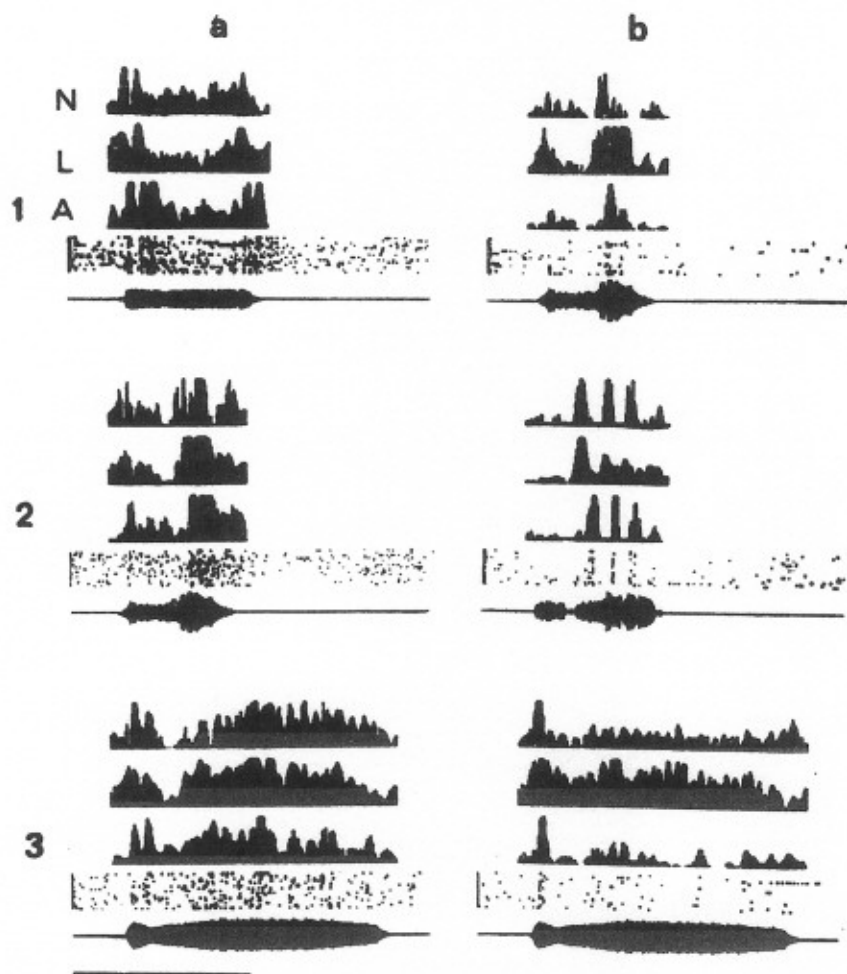


Figure 2. Predictions of responses of 6 cells (a/1-3, b/1-3) to various vocalizations. Each display consists of (bottom to top): Envelope of vocalization, raster display of responses to 15 consecutive representations of the cell, smoothed PSTH of the actual response (A), prediction to this response made by the linear model (L), prediction made by the non-linear model (N). Bin duration for the PSTH is 3 ms with moving average of 3 ms. Time scale: 0.5 s.

Notice that in the left column (a), the linear predictions are better than the non-linear ones. In the right column (b), non-linear predictions are clearly superior to the linear predictions.

predictions approximate reasonably well the actual responses when linearity is assumed (e.g. Fig. 2(a)). In other cases, the predictions made by quadratic model are clearly superior (e.g. Fig. 2(b)). In general, the non-linear model performed better than the linear one in the predictions of phasic responses, whereas the linear model was sufficient for more tonic responses (Figs 2(b-2) and 2(a-3), respectively).

This distinction between the linear and quadratic responses was based on a comparison between the quality of the predictions obtained by the two models. Such a distinction can be achieved by applying only the second order model, and comparing the relative contributions of the linear component and the non-linear (quadratic) component to the total response (Fig. 3). The ratio between the weights of the linear (Y_l) and the non-linear (Y_q) contributions in each prediction may subservise, in this case, as a measure of "linearity" of the prediction. Using this criterion, any cell in our sample could be ultimately characterized by the average "linearity" of all its predicted responses.

By correlating between the "linearity" of the various cells and their spatial

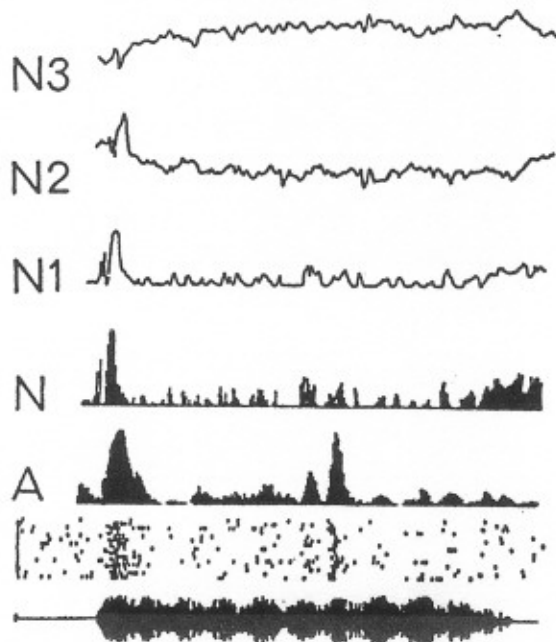


Figure 3. Linear and non-linear (quadratic) components of a predicted response, made by the second order model. Bottom to top: Envelope of the vocalization (input); raster display of responses to 15 consecutive representations of the cell (actual response). (A) Smoothed PSTH of the response. (N) Prediction of the response. (N1) Line drawing of N. (N2) Contribution of the second order kernels to N1. (N3) Contribution of the linear kernels to N1. Notice that the response is an "onset response", which is highly non-linear by definition, yet it is predicted by the model.

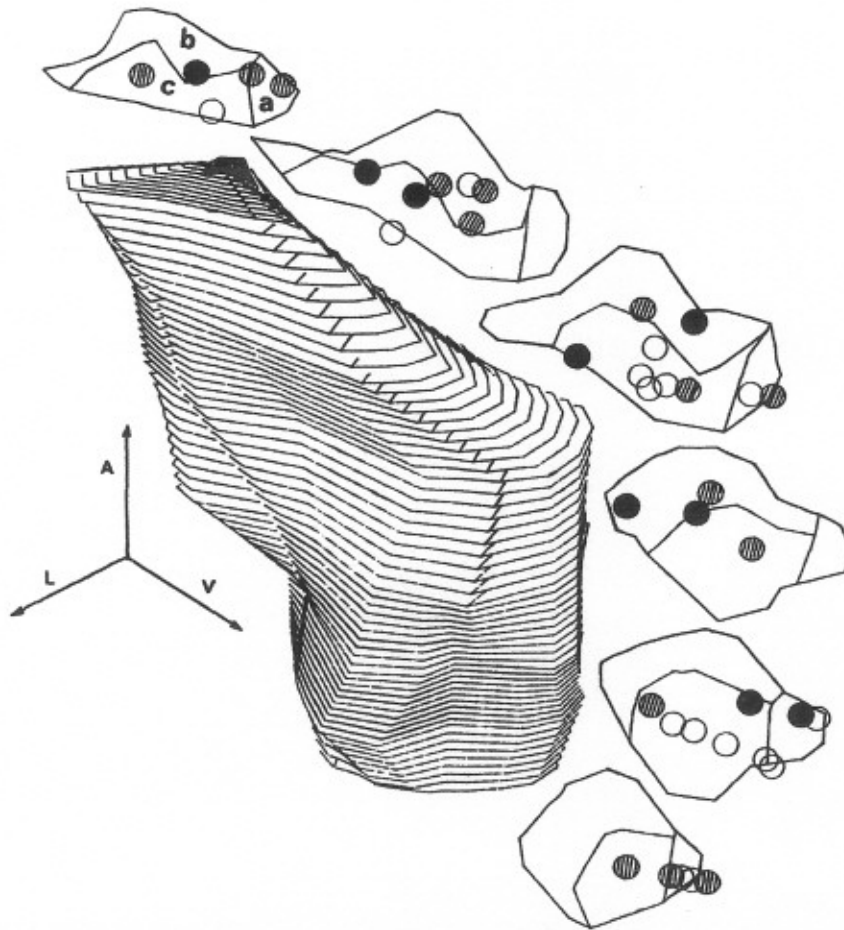


Figure 4. Spatial location of recording sites. A computer reconstruction of the MGB: a 3-D perspective view and some selected coronal sections of it. Subdivisions of the MGB denoted on the top section. Orientation axes: A—anterior, L—lateral, V—ventral. Location of recorded cells designated by circles superimposed on the sections. “Linearity” of cells marked by the darkness of the circles. For convenience, linearity of cells is categorized as high (dark), medium (shaded) and non-linear (empty circles). Notice that cells in bMGB and on the borders of cMGB and bMGB are more “linear”.

localization, we found a clear trend for a linkage between these two variables (significance level of the one way analysis of variance between “linearity” and spatial location is 0.09). Namely, the probability of disclosing linear responses *vs* non-linear responses was higher at the medial aspect of the nucleus compared with the rest of it. More specifically, using conventional nomenclature and parcellation of the MGB [namely aMGB, bMGB, cMGB (Jordan, 1973)], our findings suggest that cells located at the bMGB and at the border zone between the bMGB and the cMGB (comparable to the pars lateralis of the

vMGB) are more "linear" in terms of their responses to intraspecific communication sounds, compared with the rest of the nucleus (Fig. 4).

Structural and physiological distinctions between the mMGB and the vMGB have already been demonstrated in the past (Allon *et al.*, 1981; Jordan, 1973; Aitkin, 1973). Our results, albeit from a completely new point of view, are clearly supported by these findings. Very intriguing in this regard is the fact that the bMGB is a polysensory neuronal substrate, whereas the other subdivisions belong to the main auditory pathway.

Summarizing our findings, we suggest the existence of at least two modes of processing along the auditory pathway (probably induced by the connectivity along the network), that operate concurrently. These processes can be approximated by a linear model and by a non-linear one. This functional distinction, which is manifested also in the spatial organization of the MGB, is in accordance with various physiological and anatomical features which have been demonstrated in the past.

The functional significance of multiple processing of an auditory signal in the MGB is still not clear. However, as in other auditory structures (Evans, 1974; Suga, 1982; Fitzpatrick and Imig, 1982), we assume that it is related to the parallel processing of different tokens and information embedded within a complex communicative sound. Processing of a single input along parallel channels or subsystems is very probable, and the mode of processing is not necessarily uniform in all the channels. It might be associated with various degrees of complexity of which linear and non-linear transformations are only one of its manifestations. In this regard, our findings represent a new revelation of this general concept.

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