

Identification of MGB Cells by Volterra Kernels

I. Prediction of Responses to Species Specific Vocalizations*

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Abstract. The function of CNS sites is frequently explored by an analysis of its input-output relationships. However, such research are often confined to a qualitative and subjective inspection of raw data. System Identification methods can be used to formalize the stimulus – response relations, and one of them, the Volterra approach, is employed here in order to define these relations in the MGB of the squirrel monkey, natural vocalizations being the stimuli. In order to validate the formal representation of the system under study, the predictability power of the model is tested. Having the distances between responses (PSTH) and predicted response quantified, it is found that the predictions made by the model are, in general, “closer” to the actual responses than some arbitrarily chosen responses. It is concluded that there are cells in the MGB that can be characterized by their Volterra kernels, and further research on the cell’s functional role can be based on these kernels.

Introduction

Characterization of stimulus response relations in the CNS is a central aspect in experimental neurobiology. However, due to the complexity and apparent nonlinearities in these relationships, especially at higher levels of the brain, experiments often do not go far beyond the description of raw data or of fundamental quantitative analyses.

In an attempt to disclose the role of primate MGB in the processing of complex auditory stimuli, in particular intraspecific communication sounds, we have recently analyzed stimulus-response relationships of single cells (Allon et al., 1981) located at

different regions of that nucleus. Our model system was a squirrel monkey (*Saimiri sciureus*) which was selected for that purpose on the basis of its very rich vocal repertoire which subserves this species for intraspecific communication (Winter et al., 1966).

Among other observations we noticed that, in some cases, the temporal distribution of “response peaks” corresponded in time with some transients of the stimulus (see also Creutzfeldt et al., 1980; Glass and Wollberg, 1983). This “peak tracing” phenomenon, which is best illustrated by the similarity between the response pattern of the cell and the envelope of a particular spectral component of the call corresponding to the characteristic frequency of the cell (Fig. 1), was, however, confined to a relatively small number of cells. For most other cells this phenomenon was not readily seen, and probably obscured by other components of the response, even if existed.

These results fit very well with a spectro-temporal model, suggested recently (Creutzfeldt et al., 1980) for the detection of complex sounds by cell assemblies in the thalamocortical segment of the auditory system. Such relationships are also not totally unexpected in the light of the well known filtering properties of single cells along the auditory pathway, including the MGB (Allon et al., 1981), but certainly call for a more formal and quantitative description. The fact that for most cells relationships of that kind are not readily observed, argues strongly for a more sensitive method to be applied, and for a quantitative description of the transfer characteristics of stimuli into response signals. This last aspect, which is often defined as “System identification” is one of the basic goals in the present study. Various approaches and techniques have been suggested for the identification of biological systems, among which the Volterra and the Wiener-Volterra representations and their variants are most widely applied both to peripheral (Marmarelis and Marmarelis, 1978) and central (Aertzen, 1981; Eggermont

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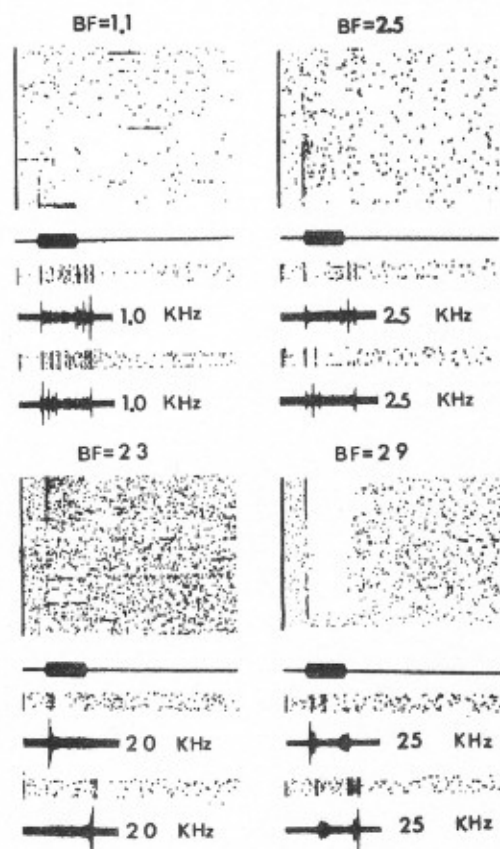


Fig. 1. An illustration of the "Peak tracing" phenomenon. Response patterns of 4 MGB cells elicited by the call "Peep" (PL) and its corresponding "Ilac" (LP). Each cell is represented (top to bottom) by: its characteristic frequency (BF); a raster display of responses to pure tones (at an intensity of 80 dB SPL) ranging between 0.5–32 kHz; envelope of the pure tone burst; response pattern to the call "peep" represented by a raster display of 15 consecutive trials; envelope of a filtered frequency, approximately corresponding the BF of the cell; response pattern to the Ilac (LP); envelope of the filtered frequency

et al., 1983) neurons. A detailed review of such applications can be found in Hung and Stark (1977).

These methods formalize the input to output transformation by obtaining a functional description of the transformation as an operator on the functions space. Volterra presented the main theory (1930), and Wiener showed (1958) how the operator can practically be evaluated, using a white Gaussian noise as a stimulus.

The requirement of the Wiener approach on the input to be a white Gaussian noise is the main reason we preferred the Volterra approach. This requirement resides in the assumption that if the duration of the stimulus is long enough, there is a finite probability that any given stimulus waveform is represented by some sample of the white noise, and thus it is conceivably the best representative stimulus and the most

effective one. This argument has proven to be valid for some sensory systems, mainly for their peripheral aspects (Marmarelis and Naka, 1972–1974).

However, it is not necessarily the case for higher levels of the brain, where functional networks associated with the detection of sensory stimuli have been developed and selected during evolution according to the biological survival values of these stimuli. With regard to the auditory system, other auditory signals might be more effective than white noise. Tentative candidates for that purpose are natural vocalizations which are used by animals for inter- and intraspecific communications (Capranica, 1972; Artzen, 1981). Indeed, earlier studies with squirrel monkeys have proven that such vocalizations are more effective in eliciting responses in single auditory cells both in the MGB and the auditory cortex (Allon et al., in preparation; Newman and Wollberg, 1973; Winter and Funkenstein, 1973).

Any attempt to formally describe input-output relations of a biologic system faces a fundamental problem concerning the determination of its boundaries. In our case, the most basic output function would be a response of a single MGB cell. Since the input to each cell is not at our disposal, the boundaries of the "system" have to be extended. The most extreme boundaries will thus be the peripheral aspect of the auditory system (namely the ear) on the one extreme, and the single MGB cell whose activity is recorded on the other extreme. Such a system comprises a whole functional network of cells culminating in a single MGB cell. In this case we deal with as many "systems" as the number of recorded MGB cells. However, considering some redundancy, and assuming the existence of functional cell assemblies for which the total output represents the output of the system, we hopefully cut by far the number of variants.

The Volterra representation of a system is formally valid only when some conditions are fulfilled (Volterra, 1930). Some of them, such as "causality" are certainly satisfied, as we deal with a physical system. However, it is not trivial to rigorously prove the validity of other conditions such as the "Frechet continuity". Under such circumstances, namely when some of the requirements are being met while it is practically impossible to prove some others, a plausible approach to test the validity of Volterra's representation is to evaluate its predictability power. Formally, such an approach provides an answer only if the results are negative. That is, if the transfer functions of the system, determined by a given set of input-output relations, are unable to predict the output elicited by an arbitrary input to a required degree of precision, then this would mean that the system under investigation cannot be represented by these transfer func-

tions. If, on the contrary, the system's output can be predicted, then in spite of the fact that some conditions were not formally met, it is plausible to characterize the system by its Volterra representation, and further conclusions may be derived from this representation. It follows that the predictability power of the model is a necessary, though not sufficient, condition to be met.

In this study we investigate the predictability power of a certain approximate model to the Volterra representation. First, we describe the input and output to the "systems", then we present our model and the method of its identification. We conclude by a discussion of several tests of the prediction power of our model.

System Input

The system inputs consisted of 7 natural vocalizations of the squirrel monkey, representing 5 out of the 6 main vocalization groups observed by Winter et al. (1966) (see Fig. 2a).

The vocalizations were represented either normally (denoted hereafter "calls") or in reversed manner ("llacs"). The frequency range where most of the vocalizations' energy is concentrated is between 0.5 and 20 kHz. Techniques of recording and playback of the vocalizations are described elsewhere (Glass and Wollberg, 1983a).

Auditory stimuli can generally be represented in terms of acoustic energy function $P(t)$. However, if a reasonable time resolution is required, then a digitized vocalization will consist of some ten thousands values, an amount too large to be numerically manipulated.

We preferred a more practical approach, referred to as Short Time Power spectrum (Fano, 1950), where acoustic input is represented by its spectral components, each component having its temporal energy distribution.

Since the operation of the peripheral aspect of the Auditory pathway can be approximated by a bank of overlapping 1/3 octave filters (Evans, 1977), a natural choice of the spectral resolution of the frequency bands would also be 1/3 octave.

In this case, the ear is excluded from the system being identified, and the input is actually multi-input: each acoustic input is decomposed into spectral components before entering the system's boundaries.

Due to current computational limits (see Identification Procedure), the spectral components we used are based on 1 octave bandpass filters, but it is our intention to refine the model to accommodate a 1/3 octave resolution.

The spectral components were obtained by means of FFT, with time resolution of 3 ms and frequency resolution of 78 Hz. The results of the digital filtering

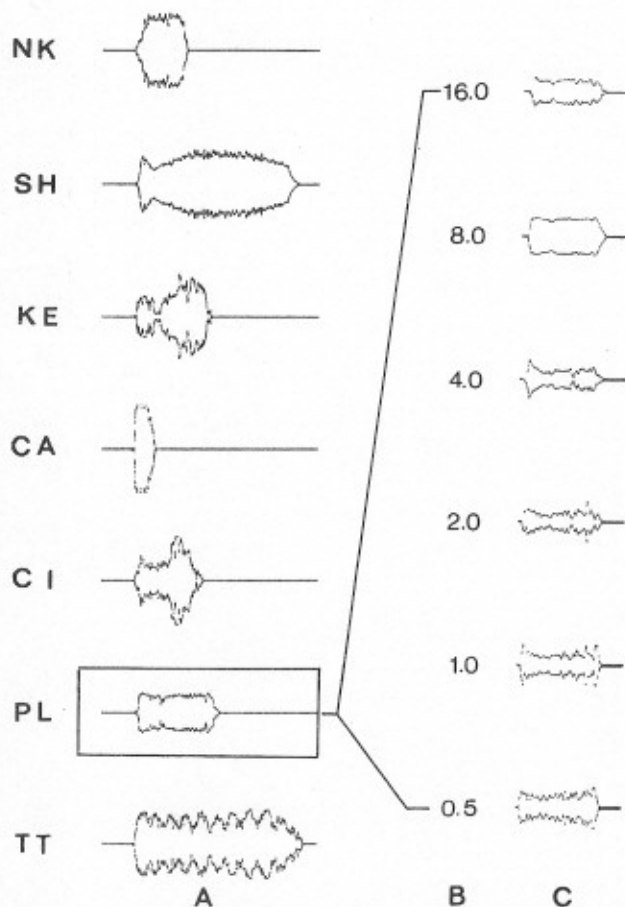


Fig. 2A-C. An illustration of the multi input system. A Envelopes of the 7 species specific vocalization employed in this study: TT - twitter, PL - peep, CI - chirp, CA - cackle, KE - kecker, SH - shriek, NK - oink (Winter et al., 1966). C Six frequency bands filtered (digitally, one octave resolution) from the call peep, yielding the envelopes from which the multi input representation of that call is extracted. B Center frequencies of corresponding filters. A similar procedure was conducted for all other calls and llacs. Scale: (length of bar crossing all the vocalizations) 1.3 s

were combined to 1 octave components, yielding 6 spectral components for each vocalization (see Fig. 2).

During the experiments, pure tones ranging in frequency (from 0.5 to 32 kHz) and intensity (down from 80 dB SPL to threshold) were also represented to the monkeys in order to obtain tuning characteristics of single MGB cells. [For further technical details see Allon et al. (1981).]

These stimuli are naturally represented by a certain spectral component, but as we are restricted to octave resolution, only the 6 tones represented by the 6 octaves are used.

System Output

The output of the system resides on the responses of single MGB cells elicited by various stimuli (system's

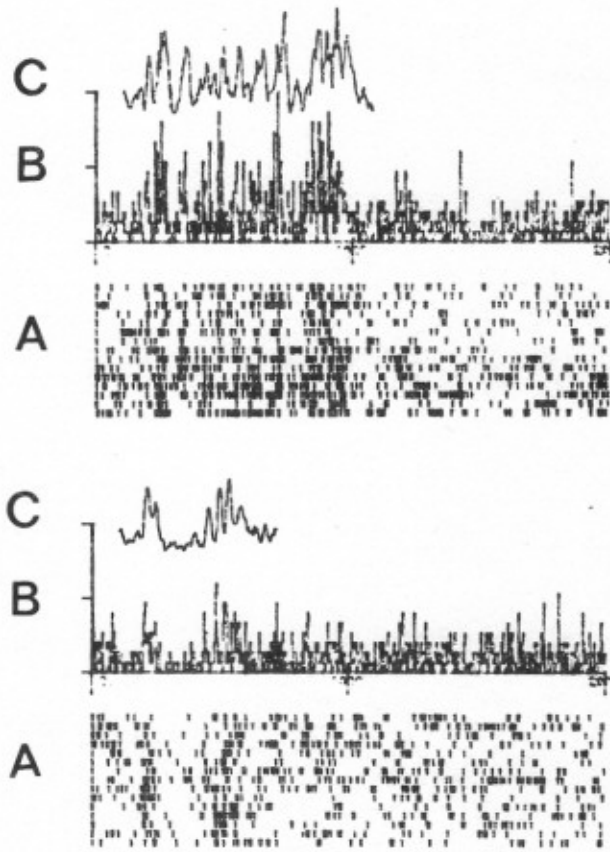


Fig. 3A–C. An illustration of responses of a single MGB cell to the vocalizations twitter (top) and chirp (bottom). A Raster display of 15 consecutive presentations of the same call. B PSTH with a 3 ms bin width. C Smoothed histogram of the response. Full scale – 2 s

input). This output can be considered as a train of action potentials (spikes).

This representation is adequate mainly when the response is highly deterministic. Generally, some averaging techniques are applied to the raw data, the most common being the peristimulus time histogram (PSTH). On that case, the unit's response is acquired several times following a given trigger, and a time histogram is calculated out of the several pulse trains.

The bin duration and number of repetitions certainly effect the PSTH, and thus the output function is not strictly unique. However, the PSTH is a well agreed description method and it is beyond the scope of this study to evaluate it as a valid and invariant representation of the output.

In the present study each stimulus was repeated 15 consecutive times, and bin duration for the histogram was 3 ms. In order to obtain a smooth output function, a moving average was applied to the basic PSTH, with windows of 3 ms. Figure 3 displays a cell's responses to two different stimuli, along with the corresponding PSTHs and the smoothed PSTHs.

Identification Method

The system we analyse is a multi-input and single output one: The inputs are the temporal energy distributions of six spectral components, denoted by $x_1(t)$ to $x_6(t)$, and the output is the smoothed PSTH denoted by $Y(t)$.

Assuming the validity of the Volterra representation for this system, its functional aspect can be described as

$$Y(t) = F\{x_1(t), \dots, x_6(t)\} \quad (1)$$

which up to a second order expansion with Volterra kernels becomes

$$Y(t) = \sum_{r=1}^6 \int_0^M H_r(\tau) x_r(t-\tau) d\tau + \sum_{r=1}^6 \sum_{s=1}^6 \int_0^M \int_0^M H_{rs}(\tau_1, \tau_2) x_r(t-\tau_1) \cdot x_s(t-\tau_2) d\tau_1 d\tau_2. \quad (2)$$

Here $H_r(\tau)$ is the linear kernel associated with the input $x_r(t)$, and $H_{rs}(\tau_1, \tau_2)$ is the "cross kernel" associated with inputs $x_r(t)$ and $x_s(t)$ (Marmarelis and Naka, 1974), and M denotes the length of the systems' memory.

In order to compute the kernels, each one is regarded as a series in $\{Q_i(t) = e^{-t} L_i(t)\}_{i=0}^{\infty}$, where $L_i(t)$ are the Laguerre polynomials, following the results of Brandsteter et al. (1971). Then each kernel is approximated by a finite number of terms in its expansion:

$$H_{rs}(\tau_1, \tau_2) = \sum_1^k \sum_1^k \alpha_{ij}^{rs} Q_i(\tau_1) Q_j(\tau_2),$$

$$H_r(\tau) = \sum_1^k \alpha_i^r Q_i(\tau), \quad k=6. \quad (3)$$

The system of equations which determines the unknown coefficients in (3) is obtained as follows:

(i) The expressions in (3) for the kernels are substituted into (2) to yield the relation

$$Y(t) = \sum_r \sum_i \alpha_i^r a_i^r(t) + \sum_r \sum_s \sum_i \sum_j \alpha_{ij}^{rs} a_i^r(t) a_j^s(t), \quad (4)$$

where

$$a_i^r(t) = \int_0^M x_r(t-\tau) Q_i(\tau) d\tau.$$

The number of unknowns in (4) is $6k$ of the form α_i , and $21k^2$ of the form α_{ij} . These unknowns are formally organized into a vector α .

(ii) Each vocalization $X^{(i)} = \{x_1^{(i)}, \dots, x_6^{(i)}\}$ and the corresponding smoothed PSTH $Y(t)$ are considered on a discretized set of equidistant points in time $0 < t_1 < \dots < t_n$, with the parameter n being limited by the resolution of the measurements.

(iii) For each input-output pair, Eq. (4) is considered in times t_1, \dots, t_n , with the integrals replaced by numerical quadratures. Thus each such pair determines n linear equations for α .

(iv) With the substitution of enough input-output pairs the number of equations increases, while the number of unknowns stays fixed. A sufficient number of input-output pairs are included to yield a significant overdetermined system, formally described as

$$A\alpha = Y. \quad (5)$$

In (5), A is a matrix computed from the input $x_r^{(i)}(t_j)$ and the functions' values $Q_i(t_j)$, and Y consists of the discrete values of $Y^{(i)}(t_j)$. The row dimension of A depends on the total duration of the inputs included, while the column dimension depends on the dimension of α . In order to enforce a strict overdetermined system, we considered only "adjacent" cross kernels, i.e. H_{ij} with $i-j=1$ and neglected the other cross kernels H_{ij} with $i-j \geq 2$. This led to a matrix of 1099 by 342.

The set (5) is solved by least squares for α , and the kernels are determined by (3).

The numerical evaluation of α consumes a considerable amount of computation time on a large scale computer (CDC CYBER 855), and special software was developed in order to efficiently handle the large matrices involved.

A significant saving in the computation of the kernels for several different cells is gained by the observation that the matrix A depends only on the inputs $X^{(i)}(t)$ and on the expansions (3), but is independent of the output $Y^{(i)}(t)$ of the cell. Therefore, as long as the inputs used to determine the kernels are fixed for all the cells, it is useful to calculate the pseudo inverse of A , \hat{A} , only once. Thereafter, computation of the cell's kernels is simply a matter of computing $\hat{A}Y$, with the vector Y characterizing the output of the cell.

Having the coefficients vector $\alpha = \hat{A}Y$ obtained for a certain cell, it is possible to compute the output predicted by our model to a given stimulus $X'(t) = \{x'_1(t), \dots, x'_6(t)\}$ by

$$Y' = A'\alpha. \quad (6)$$

Here A' is computed similarly to A , but with respect to the given input functions $X'(t)$ only.

The predicted output, Y' , is truncated to non negative values, since the real output Y is non negative.

As was mentioned above, the available set of inputs (along with the corresponding outputs) consisted of 7 calls, 7 llacs, and a restricted form of pure tones. For each cell, the following procedures are applied:

1. The 7 calls with their corresponding PSTH's are used to obtain the kernels, by which a predicted output to the 7 llacs is calculated.

2. The 7 calls and one llac ("Kecker") are similarly used to predict the output to the remaining llacs.

3. The 7 llacs and one call ("Kecker") are used to predict the output to the remaining calls.

For several cells, the kernels computed by step 2 are used to predict the output to the corresponding pure tones.

Prediction of Responses

The obvious question concerning the quality of a prediction is to what extent is a real response "close" to a predicted one. The responses of the system being identified, namely the network culminating in an MGB cell, as well as the predicted responses, are considered here to the smoothed PSTH functions and the smoothed versions of the predicted vectors Y in (6).

Any attempt to rigorously define similarity between such responses is closely related to the issue of neural response quantification, and as such, is far from being adequately solved. This especially holds for complex response patterns, consisting of discrete time locked inhibitory and excitatory components, frequently encountered in the higher levels of the auditory pathway.

Looking for a quantification to the similarity between responses, we inevitably have to tailor a specific formulation, and not count on conventional measures, such as cross correlation. The measure we employ is related to the temporal distribution of the spikes along the response, and reflects the relative deviation of time locked patterns in the responses. This measure was found by trial and error process, in order to fit our subjective judgement of the distance between responses, and is formalized as follows:

Let the total activity of a response Y be defined by

$$S_T = \int_0^T Y(t) dt, \quad (7)$$

where T is the duration of the response (only equal length responses are compared). We aim at comparing the temporal distribution of activity along the interval $[0, T]$ of two responses - $Y(t)$ and $\tilde{Y}(t)$.

To this end we compute for the response Y the values f_1, \dots, f_m measuring the distribution of its relative activity in m equal subintervals of $[0, T]$:

$$f_j = \frac{\int_{I_j} Y(t) dt}{S_T} \quad \text{with} \quad I_j = \left[\frac{j-1}{m} T, \frac{j}{m} T \right]$$

and similarly g_1, \dots, g_m are computed for the response $\tilde{Y}(t)$. The "distance" $D(Y, \tilde{Y})$ between Y and \tilde{Y} , is then measured by

$$D(Y, \tilde{Y}) = \left[\sum_{j=1}^m \frac{(f_j - g_j)^2}{\max(f_j, g_j)} \right]^{1/2}. \quad (8)$$

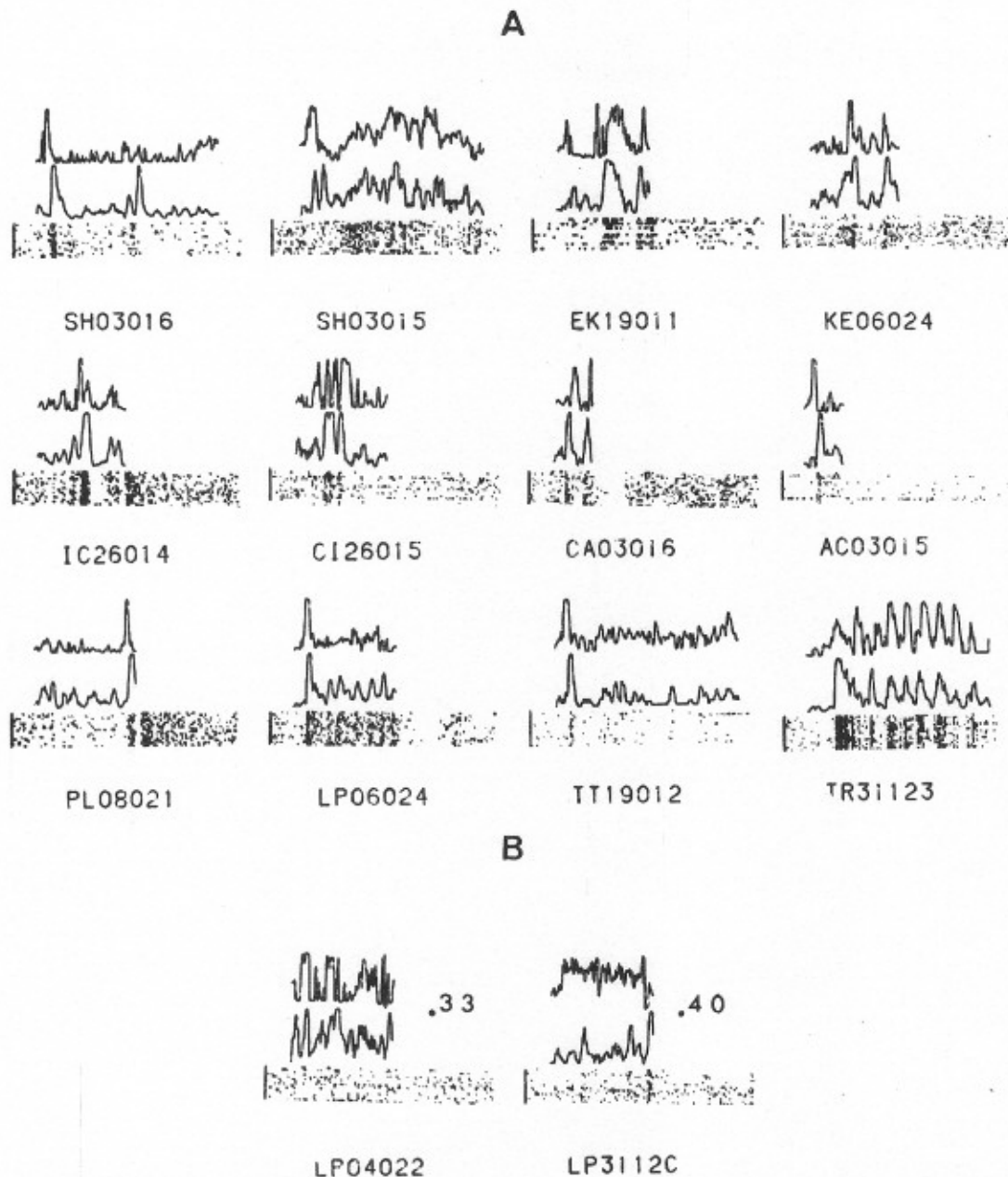


Fig. 4A and B. Illustration of predictions of responses to vocalizations. **A** Predictions we consider as "good" (distance values of 0.2–0.3). Each example consists of raster display of the real responses (lower), PSTH of this response (middle) and a prediction to the response (upper). Denoted below each example is the unit number and stimulus name (names as in Fig. 2, llacs denoted by reversed names, except for TR, which is the llac of TT). **B** Prediction we consider as fair (left) and poor (right). Distance values are denoted to the right of the PSTH. Full time scale of raster display – 1 s

The parameter m determines the refinement of the comparison. The bigger m is, finer temporal deviations are taken into account. In our tests $m = 10$.

Naturally, the extent to which a prediction fits the real response is expressed by the distance between them: the prediction is better as the distance decreases. However, classifying predictions as "good" or "poor" is

subjectively done, by determining corresponding ranges of distances.

Some examples of predictions along with the corresponding responses are displayed in Fig. 4. If we "predict" a response which was used in the identification procedure, we generally have distances of 0.2–0.3 between the "prediction" and the real responses:

actually, this distance reflects the extent to which the overdetermined system (5) can be satisfied for this response. We therefore refer to predictions with distance values of approximately 0.2–0.3, 0.3–0.4, and over 0.4 as good, fair, and poor, respectively.

Notice that while some of the predictions displayed (Fig. 4A) are good fits by any criterion, other (e.g. EK 19011) are good predictions according our judgement, although they might not be considered as such by cross correlation.

As for responses to pure tones, due to the differences in frequency resolution between the real inputs (pure tones) and our octave filtered tones, and since the stimuli were presented only once during the experiments, quantitative comparisons are impractical. Nevertheless, a qualitative comparison is possible. Figure 5 displays a prediction which reveals quite similar features to the real response.

In order to validate the predictability power of the model, we compared the quality of the predictions of the model with the quality of another type of reasonable "predictions". A natural candidate to serve as a predictor to a given response, is the envelope of the vocalization by which it was elicited.

For each cell, the envelope of each vocalization was tested as a "predicted" response to the same vocalization, and the distances of these "predictions" from the real response were compared with the distances of the model's predictions from the real responses.

As can be seen from the results of this comparison (Fig. 6), the distances between the model's predictions and the real responses are consistently smaller than the corresponding distances of the envelopes.

When procedure 2 (of "identification method") is applied, about 75% of all the responses (218 out of 287) are predicted better by the model, and this percentage increases to 80% when procedure 3 is applied. Considering the cells, for 85% of them (by both procedures) the model predicts better most (above 4 out of 7 vocalizations) of the responses.

The same comparisons, when performed not with the envelopes, but with predictions to responses of an arbitrarily chosen cell taken as "predictors", yield similar results, the only difference being a minor decrease in the percentage predicted better by the model.

The finding that there is no evident difference in the quality between calls predictions and llacs predictions (procedures 2 and 3) can be related to some of the results of Glass and Wollberg (1983a), concerning responses of Auditory Cortex cells to llacs and calls.

Another outcome of the comparison concern the validity of the model. A valid Volterra representation should yield better results as the number of input-output pairs used for evaluating the kernels is in-

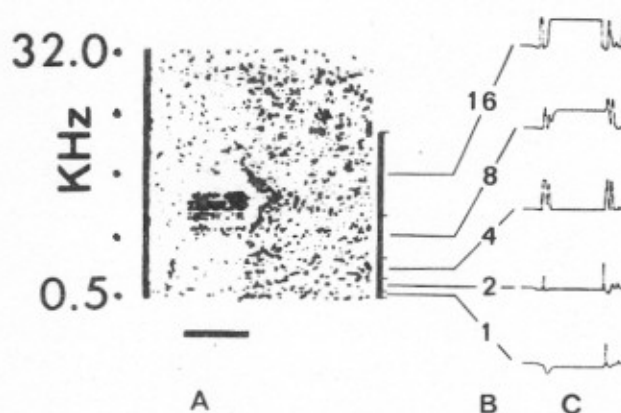


Fig. 5A–C. A prediction of response of a certain cell to pure tones. A Raster display of the real response (as in Fig. 1). C PSTH of predicted response to 1 octave bandpass filtered tones with center frequency denoted in B. The corresponding bands are marked on the horizontal bar to the left of B. Notice that the PSTH is supposed to represent the response to its corresponding band

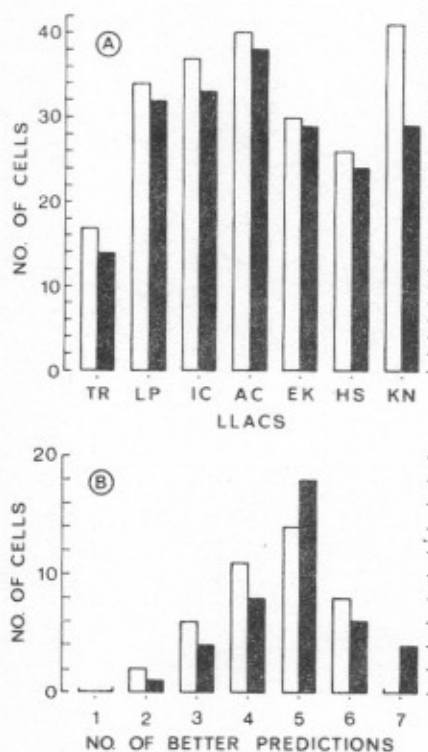


Fig. 6A and B. A comparison between the model's predictions and the vocalizations' envelopes as predictors to the real responses. A Number of cells (out of total 41) for which the model's predictions are closer (according our measure) to the real responses than the envelopes. The vocalizations are denoted below the columns. Shaded columns: predictions based on 7 input-output pairs. Blank columns: predictions based on 8 pairs. B Number of cells for which n vocalizations are predicted better by the model than by the envelopes (n denoted below the columns). Blank and shaded columns as in A. Note that in prediction based on 8 pairs, only 6 predictions are made

creased. As can be seen in Fig. 6, the results are indeed better for predictions based on 8 pairs than those based on 7 pairs. Obviously, other improving steps to be tested are a further increase in the number of input-output pairs, a refinement of the spectral resolution of the input and an upgrading of the model to accommodate kernels of order 3 and/or more terms in the expansions (3). These further steps are naturally limited by the complexity of the computation involved.

It is clear, even by eye inspection (see Fig. 4), that the predictions' qualities are not uniform. Predictions of responses of various cells to vocalizations differ in quality, as well as predicted responses of the same cell to different vocalizations. This is also evident as we analyze the comparison of the "test predictions" to the model's.

The factor behind these differences is yet unclear. We cannot rule out the possibility that in the MGB there exist some input to output transformations which cannot be presented by a Volterra series, as the requirements for this representation are not satisfied. On the other hand, these differences might stem from variations in the degree of the nonlinearities of the transformations: the current expansion might well fit some of the cells, while others can be represented only by a refined model.

In both cases, physiological characteristics such as tuning properties, latency and spontaneous activity level may supply a more definite answer. All of these are currently under further study, in order to shed more light on the functional role of the MGB.

The predictability power of our model, as demonstrated here, leads us to the conclusion that there are cells in the MGB for which the characterization of the transfer functions by Volterra's kernels is justified and promising.

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