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Identification of MGB Cells by Volterra Kernels

II. Towards a Functional Classification of Cells*

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Abstract. System Identification methods can be implemented in sensory physiology to formalize stimulus – response relationships. We apply the Volterra approach in order to define input-output relations of Medial Geniculate Body (MGB) cells in the awake squirrel monkey. The transfer functions (kernels) of MGB cells are computed using input output pairs. The inputs are intraspecific communication sounds, represented by their spectral components at a 1 or $^1/_3$ octave resolution, yielding thus a multi input system. The outputs are represented by the responses of single neurons expressed as the smoothed Peri Stimulus Time Histograms (PSTHs). The kernels are computed for various combinations of the model: linear and quadratic Volterra expansions respectively 1 and $^1/_3$ octave resolution of the input. Judging by the predictions of these models, it can be concluded that the model predictibility power is systematically improved as the order of the model and its spectral resolution are increased. An analysis of the predicted responses reveals that in certain cases, the quality of the predictions might be related primarily to either the order of the model, or alternatively to the spectral resolution of the input. The quality of the predictions, and their "Linearity", are associated with the spatial location of the cells within the MGB. Cells located at the medial aspect of the nucleus exhibit more "linear" responses, which are also better predicted, compared with most other cells.

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Introduction

System identification methods applied for describing stimulus-response relationships in the nervous system are often represented by the Volterra and Wiener-Volterra equations (Hung and Stark 1977; Marmarelis and Marmarelis 1978; Aertsen 1981; Eggermont et al. 1983). In most of these cases, white gaussian noise was applied for the calculation of the system's kernels.

In an earlier paper (Yeshurun et al. 1985), we described the application of the Volterra approach for the identification of Medial Geniculate Body (MGB) cells in the awake squirrel monkey *(Saimiri sciureus)*. In our model system, the input consisted of intraspecific communication sounds represented to the monkey normally ("Calls") and in a reversed mode ("Llacs"). The rationale for employing natural vocalizations as the input rather than white noise, was discussed in that paper. Briefly, we assume, on the basis of behavioural and physiological studies, that species specific vocalization represent a more natural and meaningful signal to the monkey than white noise. That is particular true when interest is focused in the neural processing of sounds at the upper levels of the auditory pathway (Capranica 1972; Suga 1978; Ploog 1981).

According to our approach, the input, namely the various species specific vocalizations and their reversed versions, were represented by their spectral components, thus yielding a multi input system. The system output was the smoothed PSTH based on the extra cellular recording of single cells activity.

Since we did not apply white noise as the input, the situation resembles non physiological systems, where the input is not at our control, e.g. rainfall-runoff processes (Boneh and Golan 1978). Under such circumstances the kernels are computed by solving a set of equations related to several input-output pairs (Amorocho and Brandsteter 1971).

As it is practically impossible to rigorously prove that a neural system can be represented by a Volterra series, a plausible way to validate such a representation is the evaluation of the predictions made by the model, as compared to the actual responses. In the previous paper we demonstrated predictions based on a model in which each signal was represented by 6 spectral bands (with center frequency ranging between 0.5 and 16 kHz, at a 1 octave resolution), and kernels were of the first and second order. We used 7 calls to compute the kernels and then predicted the responses to the remaining 7 llacs.

In order to validate the stability of the method, we analyzed the predictions obtained under various combinations of the order of the model versus the spectral resolution of the input. The predicted responses of these variants, beside their power in evaluating the validity of the model, can be also used as a classifying tool: since each model is assigned a set of parameters, the extent to which a certain cell's responses can be predicted by a given model, reflects the degree to which the system (which is the neural network culminating in the cell) is represented by these parameters. Thus, a response which is well predicted by a linear model can be viewed as representing a more "linear" process then a response which is well approximated only by a quadratic model. Obviously, cells which are not well approximated by the quadratic model are either represented by a higher order model (which is beyond the scope of this study), or can not be represented by the Volterra method at all. Since attributes assigned to responses can be averaged and thus be assigned to the corresponding cells, the classification can be applied also to the cells.

In what follows, the variants of the model are described, and the predicted responses of the variants are used in two modes: 1) case study, in which prominent features are displayed in order to demonstrate "order dependence" and "resolution dependence", and 2) an analysis of predicted responses of a selected model, where general trends are discussed.

Variants of the Model

The system we identify is represented, up to the second term in the Volterra expansion, by

$$Y(t) = Y_l + Y_q, \tag{1}$$

where

$$Y_l = \sum_{r=1}^{n} \int_0^M H_r(\tau)\, x_r(t-\tau)\, d\tau, \tag{2}$$

$$Y_q = \sum_{r=1}^{n} \sum_{s=1}^{n} \int_0^M \int_0^M H_{rs}(\tau_1, \tau_2)\, x_r(t-\tau_1)\, x_s(t-\tau_2)\, d\tau_1\, d\tau_2 \qquad |r-s| = <1. \tag{3}$$

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), M denotes the length of the system's memory and n is the number of inputs.

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:

$$H_{rs}(\tau_1, \tau_2) = \sum_{1}^{k} \sum_{1}^{k} \alpha_{ij}^{rs} Q_i(\tau_1)\, Q_j(\tau_2), \qquad H_r(\tau) = \sum_{1}^{k} \alpha_i^r Q_i(\tau). \tag{4}$$

The parameters we vary are the order of the kernels and the spectral resolution of the input. Thus, we consider the following variants:

P1: 6 inputs (1 octave resolution), linear kernels only, $k = 6$.

P2: 18 inputs ($^1/_3$ octave resolution), linear kernels only, $k = 6$.

P3: 6 inputs (1 octave resolution), quadratic and linear kernels, $k = 6$.

P4: 18 inputs ($^1/_3$ octave resolution), quadratic and linear kernels, $k = 5$.

In order to obtain an overdetermined set of equations for *P4* it was necessary to expand the kernels up to order 5 only. For each model (*P1* to *P4*), the kernels of all 41 studied cells were computed, by solving a set of equations based on the response of the cells to all (seven) llacs, and to one call (Oink). Then, these results were used for predicting the responses to the remaining 6 calls.

The quality of the prediction to each vocalization was assessed by evaluating the distance between the predicted response and the actual one, both represented by the smoothed PSTH. The distances between the actual responses and the predicted ones were computed by a slightly modified MSE (Yeshurun et al. 1985), and are summarized in Table 1.

The call oink (NK) was included as an input for calculating the kernels, hence, the values under its column in Table 1 are not distances between prediction and actual response, but merely reflect the extent to which the actual responses, used for the determination of the kernels, can be approximated by the model. The results shown in Table 1 reveal a gradual improvement of the quality of the predictions as the order of the kernels is increased and the spectral resolution of the input is refined. This certainly supports the validity of the Volterra representation of MGB cells. The most prominent improvement is gained between *P1* and *P2*, and this implies that, on the average, a model combining octave resolution with

Table 1. Distances between actual and predicted responses for all 41 cells. TT–NK: Codes of vocalizations. *P1–P4*: Type of models, *q/l* designate quadratic and linear models, $^1/_3$ and 1 designate the spectral resolution of the input. The numbers in the table are distances between the actual responses and the predicted ones, summed over all the cells

Type	TT	PL	CI	CA	KE	SH	NK	Total
P4(*q*, 1/3)	28.2	29.9	29.3	32.0	32.3	26.9	18.7	197.6
P3(*q*, 1)	31.5	30.6	32.0	34.0	33.7	30.0	20.7	212.9
P2(*l*, 1/3)	31.5	31.7	31.8	36.1	35.5	29.6	25.2	221.6
P1(*l*, 1)	38.9	40.0	40.1	39.8	40.4	38.8	35.0	273.3

first order kernels can not approximate the responses of MGB cells to a satisfactory extent. However, it must be emphasized that these results are of general nature, and while they apply for the total population, certain cells might have different characteristics then the average. It is possible to have a disagreement between the objective distance and the subjective judgement, especially when parts of the predicted response fit very well the original response, while other parts do not. Therefor, the distance measure is used only to reveal some general trends, while specific case studies are used to reveal specific response characteristics, as is done in the next chapter.

Order Dependence and Spectral Resolution Dependence

Taking into consideration the assumed nonlinearity of the Auditory System (e.g. Goldstein 1967; Pfeiffer and Kim 1973; Moller 1983) and the notion that the peripheral aspect of the auditory pathway can be approximated by a bank of overlapping $^1/_3$ octave filters (Evans 1977), one might expect that the quality of the predicted responses will be improved with both the order of the expansion and the resolution refinement. This phenomenon is indeed demonstrated in Fig. 1, where responses of two cells, predicted by all four models *P1–P4* are compared with the actual responses.

Notice (Fig. 1a) the gradual improvement of the predictions from *P1* (the model combining 1 octave resolution with linear kernels only) to *P4* ($^1/_3$ octave with second order kernels). The most prominent feature of the actual response is three narrow excitatory components in the second half of the response. Some of these response components are present in all 4 predictions, but they are partially masked (mainly in *P1*) by larger blocks of excitation. Only in *P4* all the excitatory and inhibitory columns emerge and last as in the actual response. This holds even for the less

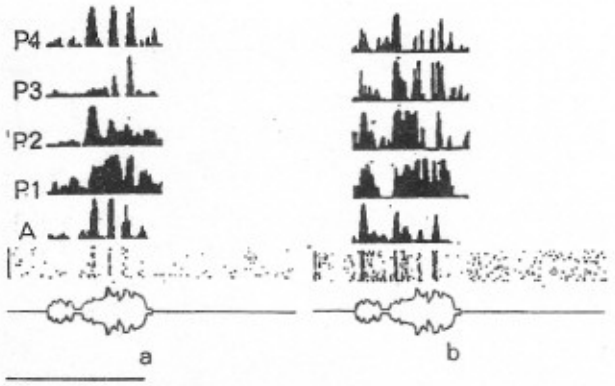

Fig. 1a, b. Predictions of the responses of 2 cells (**a, b**) to the same vocalization (KE). For each cell the display consists of (bottom to top): Envelope of the vocalization, raster display of responses to 15 consecutive representations of the call, smoothed PSTH of the actual response (*A*), predictions to this response made by models *P1* to *P4* (linear-octave, linear-$^1/_3$ octave, nonlinear-octave, nonlinear-$^1/_3$ octave, respectively). The bin duration for the PSTH is 3 ms with moving average of 3 ms. Time scale: 0.5 s

distinct components such as those at the beginning and the end of the actual response. In Fig. 1b, the same phenomenon is illustrated, yet the similarity between the details of the response and *P4* is less obvious. The prediction is improved as we go from *P1* to *P4*, but some details in the last third of the response are perhaps more accurately approximated by *P3* then by *P4*.

This illustrated improvement of the prediction by both the order of the expansion and the resolution of the inputs did not characterize, however, all the cells. In Fig. 2a and b, one can clearly see that responses predicted by models *P3* and *P4* are much closer to the actual response than those of *P1* and *P2*. The main improvement, which is most clearly demonstrated in 2a-*P3* and 2b-*P4*, is manifested in the refinement of the width (duration) of the excitatory and inhibitory components of the predicted responses, as compared to the actual response. As *P3* and *P4* are second order models, one may conclude that in these particular cases, the order of the model is more significant than the spectral resolution.

In the responses depicted in Fig. 2c, and more than that, in Fig. 2d, the spectral resolution seems to play a major role, as compared to the order of the model. *P2* and *P4*, which are based on a $^1/_3$ octave resolution, are superior to *P1* and *P3*, though it is not as prominent as in the previous demonstration. This is mainly manifested by the two excitatory components in the initial part of the predicted responses illustrated in Fig. 2c, and by the fact that the response illustrated in Fig. 2d is characterized by a marked inhibitory segment which separates between two prominent excitatory blocks.

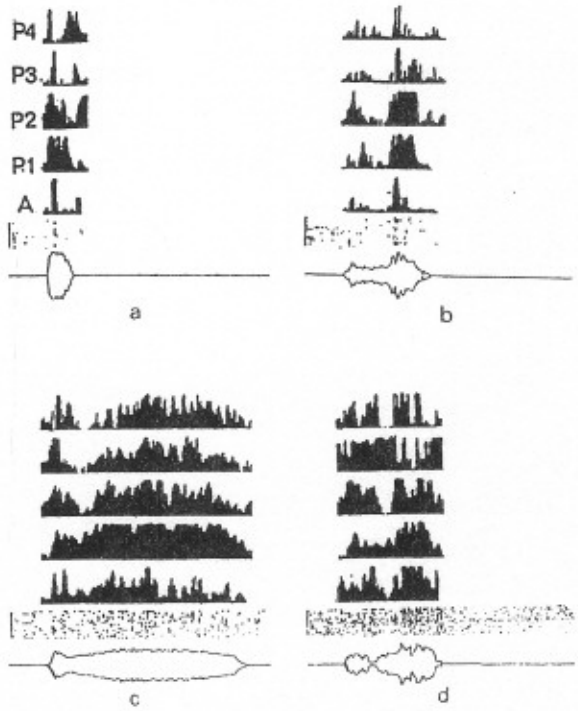

Fig. 2a–d. Effects of the order of the model and the spectral resolution on predicted responses. An illustration of the actual responses and predicted responses of 4 cells (**a–d**) to 4 vocalizations (CA, CI, KE, SH respectively). Details of displays as in Fig. 1

Computed Parameters and Anatomical Parameters

In the previous section we defined two properties of cells, determined by their identified kernels: 1) the "quality" of the predicted responses measured by the distance between the authentic response and the corresponding predicted response, and 2) the "linearity" of the cell, based on a qualitative measure of the degree to which the linear and quadratic models approximate the actual response. In a second order model, like *P3*, the "linearity" of a predicted response can be also estimated quantitatively by the contribution of the linear kernels and the quadratic kernels to the total predicted response. We define the "Quadratic factor" of a prediction Y as:

$$F_q(Y)=\frac{\int |Y_q(t)|\,dt}{\int |Y_l(t)|\,dt}.$$

Notice that this factor is well defined for our purposes (i.e. a second order model with non zero linear contributions), but should be normalized if it is applied to a general system. The "linearity" of a given response is expressed by this factor, since a response is more "linear" as this factor decreases. Since every single predicted response, of any individual cell, can be characterized by the two parameters, quality and linearity, each cell, as an entity, can be characterized by the mean quality and by the mean linearity, measured over all its predicted responses (i.e. the mean over 6 predicted responses). Averaging the "linearity" and "quality" over all responses is justified by the assumption that each cell can indeed be described by an operator which can be approximated by a second order Volterra series, and therefor these attributes can be handled as any "physiological" attributes which can be assigned to the cell and averaged over several responses. Clearly, these two parameters are not independent of each other since in a second order model, first order responses should be predicted better then second order ones. Indeed, this is the case in our system. The Pearson correlation between these parameters was found to be 0.53 (nonsignificant), but the general trend is detected in the plot of these parameters (Fig. 3A). It can be seen that generally speaking, cells are predicted better when they are more "linear".

The two kernels' dependent parameters, quality and linearity, reflect essentially some inherent pro-

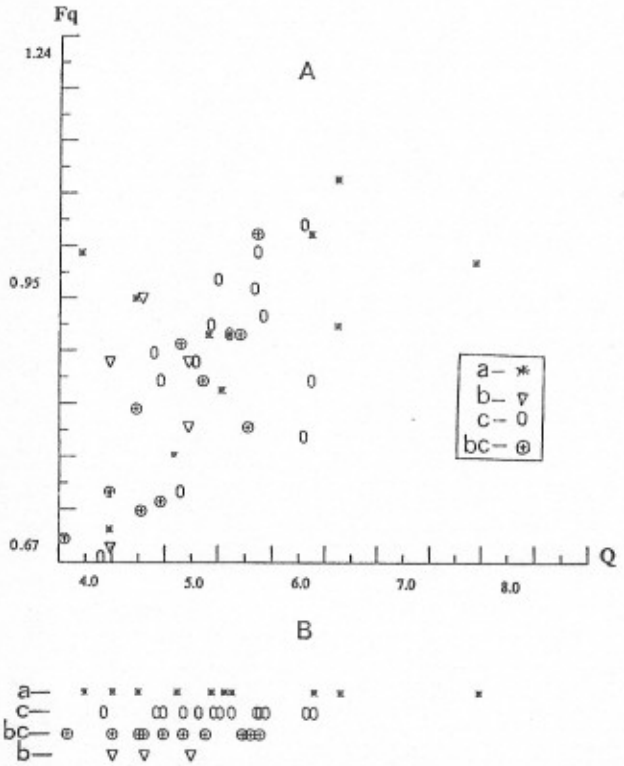

Fig. 3A, B. Values of computed parameters of the cells. Parameters are: quality (Q axis) in terms of distances between predicted and actual responses, and linearity (L axis) in terms of F_q. **A** Each symbol represents the quality and linearity assigned to a MGB cell. The symbol designates the location of the cell in one of the MGB subdivisions. **B** Quality of the prediction, data is sorted by location of cells in the subdivisions

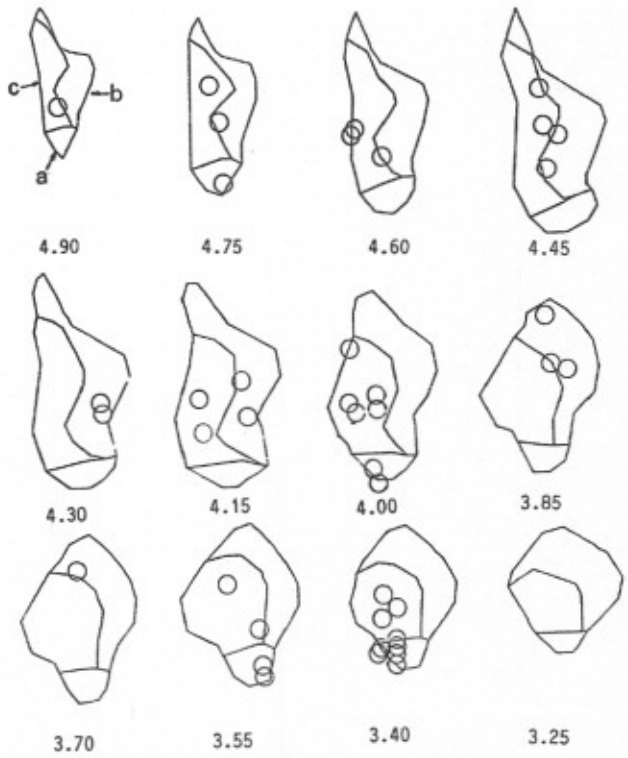

Fig. 4. Computer reconstruction of the cells location in the subdivisions of the MGB, superimposed on consecutive coronal sections. The number below each cross section designates the Anterior-Posterior stereotaxic location of the cross section. MGB subdivisions *a–c* are designated on the top left section

perties of each individual cell. Thus, in accordance with our ultimate goal, we considered it useful to correlate them with other, more conventionally obtained, cellular properties. For this purpose we selected, as a start, three physiological parameters and a structural one: 1) spontaneous firing rate; 2) characteristic frequency (CF); 3) Sharpness of tuning expressed by Q_{10db} and Q_{30db} values; 4) spatial location of the cell within the MGB.

Regarding the three physiological parameters, correlation factors between them and the computed parameters (quality and linearity) ranged between ± 0.35, and were non significant.

As for the spatial location, a very intriguing result emerged from this correlation analysis. The spatial location of each cell can be referred to one of the major subdivisions of the MGB. Different terminology has been employed in the literature for defining this parcellation. Because of conveniency, we adopted the nomenclature and parcellation introduced by Jordan (1973). A detailed description of the various parcellations and of a computerized method for locating the cells can be found in earlier publications (Allon et al. 1981; Yeshurun et al. 1981).

Table 2. Distribution of quality (mean Q) in terms of the distances between predicted and actual responses, and quadratic factor (mean Fq) of predicted responses along the subdivisions of the MGB. sd – standard deviation. Significance level of the one way analysis of variance test is 0.02 for the quality (Q), and 0.09 for the quadratic factor (Fq)

Subdivision	n	Mean Q	sd	Mean Fq	sd
aMGB	11	5.52	1.18	0.90	0.08
bMGB	5	4.41	0.49	0.80	0.07
cMGB	15	5.54	0.83	0.89	0.13
b/cMGB	10	4.70	0.66	0.83	0.09

Figure 4 describes the spatial location of all 41 cells which were considered in the present study, distinguishing between the three major subdivisions. Table 2 summarizes the distribution of the computed parameters according to this parcellation. One can see that there is a significant gradient of quality running down from "high quality" in the medial aspect of the nucleus (bMGB) to "low quality" in the lateral aspect of the nucleus (cMGB), with intermediate values in the border zone between these two (b/cMGB). As for the linearity, a similar trend (though not statistically significant) was discerned with bMGB and b/cMGB cells being more "linear" than cMGB and aMGB cells. The latter is not unexpected, since quality of prediction and linearity are probably not independent of each other.

The non uniform distribution of the computed parameters along the subdivisions can also be deduced from another aspect of Fig. 3A, if the spatial location of the cells (depicted by symbols) is considered. This distribution is even more emphasized, if only quality and spatial location are considered (Fig. 3B).

Multiprocessing in the MGB

The main difference between our approach to the problem of neural systems identification and the prevailing approaches is the use of intraspecific communication sounds instead of white noise, as the stimuli which elicit the responses, by which the kernels are calculated. The results shown here suggest that the kernels obtained by this method are "stable", in the sense that variations of parameters such as order of the kernels and the number of inputs (i.e. spectral resolution), has moderate effects on the global behaviour of the kernels (as is reflected by the predictions). On the other hand, predictions made by the variants of the model can differ markedly for specific cells, since predictions made under various assumptions are probably related to some inner mechanisms of the system which are manifested in these cases. The quality of the

predictions is not uniform, not for all the cells and not for all the vocalizations. There are responses which are, expectedly, predicted better by the nonlinear and high resolution model, in accordance with the general trend (Table 1). Yet, there are responses which deviate from this trend, and might be described primarily as "order dependent", and others, though less prominent, which are more "spectral resolution dependent". These might represent two modes of processing: a quasi-linear mode based on sharp spectral resolution, and a nonlinear but less "sharpened" process.

The fact that cells of the bMGB and b/cMGB are predicted significantly better then the others, and are more "linear", might be related to this duality. In previous studies it was found that bMGB differ from other MGB cells by their response latency, spontaneous firing rate, and by the complexity of the responses elicited by natural vocalizations (Symmes et al. 1980; Allon et al. 1981; Allon and Yeshurun 1985). The findings described in the present study are based on the kernels of the cells, and therefor are related to the transformation taking place. It can be concluded that, by and large, the processing represented by the bMGB "system", i.e. the pathway culminating in bMGB cells, is probably of a lower order than the processing of other subsystems.

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