Stimulus Reconstruction from Nonlinear Neuronal Encoding

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Abstract— **The amount of information processed by the sensory system limits the extent of an organism's perception. In consequence, stimulus reconstruction algorithms are of practical importance in quantifying the content of encoded sensory signals. Recent efforts in this way have made use of reverse Wiener (linear) filters to estimate the encoded stimulus via observation of the neural response. Experimental evidence, however, points to the existence of various non-linearities in the input-output behavior of the sensory pathway; it is therefore expected that non-linear estimation methods extract greater amounts of stimulus-related information from observed responses. Additionally, reverse filters do not provide information with regards to the forward encoding mechanism. Motivated as such, we present a two-stage framework to: (1) model the non-linear forward encoding process through a Volterra/Wiener series expansion, and (2) on this basis develop a Bayesian estimation algorithm for decoding. This approach, on the other hand, is directly linked with the forward encoding mechanisms and also improves upon the reverse-filter method in a variety of cases. Results also suggest that the above framework may be applicable in describing general non-linearities in neuronal encoding that have been observed experimentally in a variety of sensory pathways.**

Keywords— **stimulus reconstruction, nonlinear encoding, Wiener/Volterra series**

I. Summary

EFFORTS in the way of stimulus reconstruction are relevant in the context of determining the limits of sensory perception. Recent efforts in the way of stimulus reconstruction in general have focused on reverse linear filters based on the correlation structure between the response and stimulus [1], [2], [3]. An attractive of this approach is that spike trains are used as inputs into a decoding scheme; however, the knowledge of the system at hand is implicit, so that direct insight into the coding mechanism is not immediately apparent. It has also been shown that [4], [5] many sensory pathways possess nonlinear filtering characteristics, and therefore it is expected that nonlinear encoding-decoding models provide significant information in this regard.

An arbitrary sensory system is hereby thought of as a non-linear dynamic system taking sensory stimuli as input and producing neural action potentials (or firing rate) as output. The framework of this study follows a two-stage approach that utilizes Bayesian inference to estimate the stimulus. In the first stage, models of the encoding process are developed. The input stimulus is the continuous input waveform used during experiments. Neural activity is taken as the output, where the activity can be averaged into a continuous firing rate (equivalently, an inhomogeneous intensity rate for a the spiking point process). One class of systems consists of a linear kernel followed by a static nonlinearity with additive noise (i.e., the *Wiener system*, see Figure 1); presence of the static nonlinearity is motivated by the fact that firing rate (or the intensity function) is a non-negative quantity.

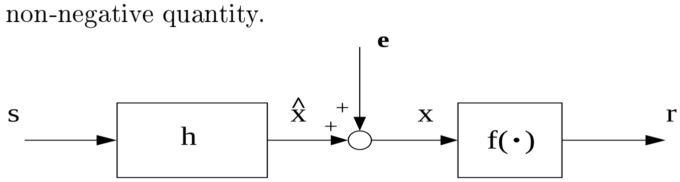

Fig. 1. The Wiener-System Cascade. h denotes the linear kernel, whereas $f(\cdot)$ refers to the static nonlinearity, which in this case is a half-wave rectification setting negative inputs to zero and passing through positive values.

The second class of systems is comprised of parallel arrangements of linear and higher order kernels, so that the stimulus ($\mathbf{s}$)-response ($\mathbf{r}$) relationship is modeled as a Volterra series expansion (see Figure 2, top), which can be expressed as:

$$\begin{aligned}\mathbf{r}(t) &= h_0 + \int_0^t h_1(t-\tau)\mathbf{s}(\tau)\,d\tau \\ &\quad + \int_0^t \int_0^t h_2(\tau_1,\tau_2)\mathbf{s}(t-\tau_1)\mathbf{s}(t-\tau_2)\,d\tau_1\,d\tau_2 \\ &\quad + \ldots + \mathbf{n}(t) \\ &= \sum_{i=0}^{M} \mathbf{H}_i(\mathbf{s}(t)) + \mathbf{n}(t)\end{aligned}$$

Here $h_i(\tau_1,\ldots,\tau_i)$ are i^{th} order Volterra kernels that can be estimated, along with the linear kernel of the Wiener system, by way of the orthogonal search algorithm [6].

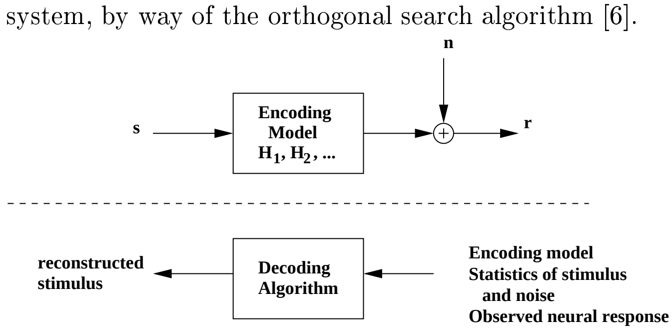

Fig. 2. General Encoding Model. The top figure demonstrates the nonlinear encoding model described in the text: H_1, H_2, etc. refer to the Wiener/Volterra functionals described above. The bottom figure outlines the two stages involved in the decoding algorithm.

In the second stage (see Figure 2, bottom), an estimator for the input stimulus is developed that utilizes the recorded noisy response, a knowledge of the underlying stimulus (developed above) and the statistical properties of the noise and stimulus (i.e., $p_{\mathbf{s}}(s)$ and $p_{\mathbf{n}}(n)$, where they denote, respectively, the probability density for stimulus and noise waveforms). The Bayesian approach can be used to obtain different estimators (e.g., the minimum mean-squared-error (MMSE) estimator defined as: $\hat{\mathbf{s}}_{MMSE} = E\{\mathbf{s}|\mathbf{r}\}$ and the maximum *a posteriori* (MAP) defined as $\hat{\mathbf{s}}_{MAP} = \arg\max_s p_{\mathbf{s}|\mathbf{r}}(s|r)$) [7]. In practice the stimulus waveform is discretized, and since the MMSE estimator requires integration over all time points, it is impractical to implement. The MAP estimator was chosen since it requires a relatively efficient multi-dimensional maximization and is henceforth referred to as the forward (FWD) estimator.

It was found that the the quality of this type of reconstruction (e.g., as for example determined by correlations between the reconstructed and actual stimuli) was at least as high as that obtained by the reverse-filter method for a variety of nonlinear systems. Figures 3 and 4 demonstrate examples of the reconstructions carried out for the Wiener system and a third-order system.

The simulations procedures for both cases are as follows; both stimulus and noise data series are defined as realizations of Gaussian white-noise (GWN) with prescribed mean and variance using a pseudo-random number generator. The simulated response is determined from the assumed encoding dynamics (i.e., kernels) and the noise process. Independent modeling and validation data sets are generated in this manner. The modeling set is then used to estimate the forward kernel, as well as the reverse filter (see [8], [7] for discussions on the estimation algorithm). At this point, the validation data set is used to carry out the stimulus reconstruction.

Measures of correlations and normalized mean-squared-error (NMSE) were computed (using the true input stimulus) to compare the FWD estimate's performance with that of the reverse-filter (RF). Here, the NMSE measure is defined as $\frac{\|\mathbf{s}-\hat{\mathbf{s}}\|}{\|\mathbf{s}\|}$, where $\mathbf{s}$ and $\hat{\mathbf{s}}$ are the actual and estimated stimuli, and $\|\cdot\|$ refers to the standard 2-norm. In both cases, the FWD estimator yields more accurate reconstructions in terms of the computed measures.

The MAP and the RF estimates are identical in the case of a linear filter, given white-Gaussian noise and stimuli, as can be shown analytically. Moreover, in cases where even-order kernels exist, the quality of the reconstructions suffers significantly due to the inherent non-linearity of the encoding mechanism; such an effect is visible for both FWD and RF estimators, and the FWD estimator's performance is at least as accurate as that of the RF in such cases.

The results demonstrate what is intuitively expected; namely, the utility of a nonlinear decoding process in the face of nonlinear encoding. More importantly, however, the incorporation of the forward encoding models within the decoding process serves as a bridge between the seemingly non-physiological reconstruction of sensory stimuli and the physiologically based encoding processes.

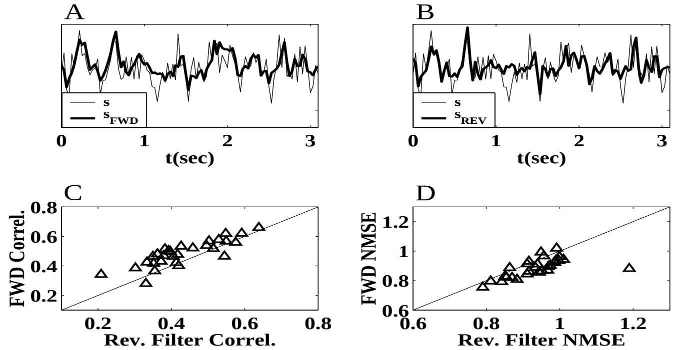

Fig. 3. Dynamical Wiener System. **A**: The actual stimulus (thin) is superimposed onto the MAP estimate of the waveform (thick); **B**: The actual stimulus (thin) is now superimposed onto the RF estimate (thick). **C**: For 25 trials, the correlation coefficients between the stimulus and the MAP estimate are plotted vs. those between the RF estimate and the stimulus; **D**: The same procedure is carried out for both MAP and RF estimates, this time using the NMSE measure between them and the actual stimulus.

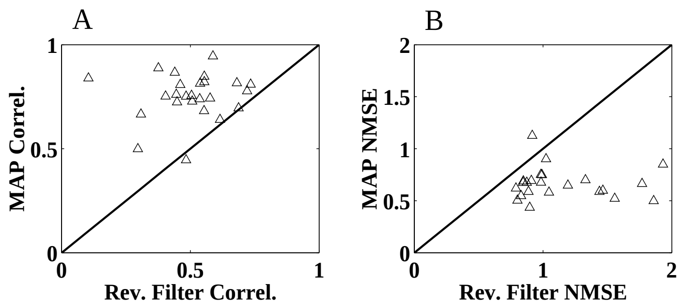

Fig. 4. Repeated Trials - MAP and Reverse Filter Estimates - Third Order Kernel. Results of 25 simulations. **A**: It is apparent that compared with the RF estimator, the MAP estimator produces estimates that on the average display higher correlations with the actual stimulus. **B**: It can be further inferred that the MAP estimators generally have lower NMSEs, as compared with the RF estimators.

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