**Distributed Coding by Single Spikes in the Bullfrog Vestibular Nerve: A Basis for Dynamical Computation in Neural Systems.**

M.G. Paulin[1], L.F. Hoffman[2] and C. Assad[3].
[1] Department of Zoology and Centre for Neuroscience, University of Otago, New Zealand. [2] Division of Head and Neck Surgery, UCLA School of Medicine, Los Angeles, CA. [3] Bio-Inspired Technologies and Systems Group, NASA - Jet Propulsion Laboratory, Pasadena, CA.

**Abstract**
Using an information criterion to fit models to bullfrog vestibular neurons, we found that optimal windows for firing rate estimation typically contain just one spike.  The implication, that single spikes transmit information, was confirmed by estimating conditional probability density functions for head state at spike times during rotational noise stimulation.  The conditional pdfs have smaller entropy than the unconditional distribution, indicating that individual spikes carry in the order of 1 bit of information about head state.  Based on this we quantify distributed coding in the vestibular nerve in terms of single spikes as assertions about head state, and show how statistical signal processing and dynamical systems methods can be applied to spiking neural systems.

## 1. Introduction

In the bullfrog, *Rana catesbeiana*, about 1200 neurons transmit information about head rotation from each semicircular canal to the brain.  There is a wide variety of response properties, with varying phase and sensitivity during rotation at different frequencies.  The large number and behavioral diversity of these neurons is curious, since each canal measures just one degree of freedom of head motion.  An engineer would run only one signal lead from the sensor.

Distributed coding in the vestibular nerve can be explained by a combination of redundancy, replication and specificity.  Redundancy means surplus neurons are available in case of local failure.  This may not be a very important design consideration, because it entails a cost and local failure may be rare.  Replication allows reduction in variance when individual measurements are noisy.  This is no doubt a factor, but variation in response properties among these neurons is systematic and reproducible, with relatively little randomness.  Thus the ever-popular  "population firing rate vector" is not a realistic candidate for representing the signal in this nerve.  We aim to characterize the specificity of individual neural responses and their role in central computation.  We have re-examined coding in the vestibular system, using modern computer-intensive signal processing and system identification methods.

## 2. Information in Spikes

From information-theoretic and signal-processing considerations, the optimal method for estimating regularly-sampled firing rates from spike timing data is to apply a digital

convolution filter with a Gaussian kernel [1]. So-called gaussian local rate estimation has a parameter σ, which determines the filter bandwidth or, equivalently, the smoothing window diameter. It spans the continuum between precise timing ( [✕] ) and average rate ($\sigma \rightarrow \infty$). Diameter σ can be estimated by cross-validation using information gain per spike [2],

$$I_S = \sum_{k=1}^{N} \left[ s_k \log_2 (r_k \Delta t) + (1 - s_k) \log_2 (1 - r_k \Delta t) \right] - N \log_2 [(r\Delta t)^{q\Delta t} (1 - r\Delta t)^{(1-q\Delta t)}],$$

where $s_k$ = 1 if there is a spike in the $k$th sample period and zero otherwise; $r_k$ is the estimated gaussian local rate; and $r$ and $q$ are the average firing rates in the fitting and validation spike trains respectively, i.e. (*number of spikes*)/(*duration of record*).

Information gain per spike measures how much additional (or, conceivably, less) information is provided about spike timing in a validation dataset by gaussian local rate estimation than by average firing rate. Statisticians will note that $I_S$ is normalized log-likelihood, and therefore maximizing information gain per spike is equivalent to statistical model selection by crossvalidation with maximum likelihood. This reinforces the suggestion that *max* [✕] is a general criterion for comparing models of spiking neurons [2].

We subjected bullfrogs to broad-band (0.05-2Hz) rotational velocity white noise stimulus and recorded spike trains from semicircular canal afferent neurons. The neurons have average maximum information gains of 0.40 bits per spike (range 0.07-0.85 bits). The estimated mean optimal rate estimation bandwidth is 1.6 times the spontaneous firing rate (range 0.52–2.6). This means that the optimal smoothing window for rate estimation typically contains only about 1 spike. It implies that information is transmitted in packets associated with spikes.


### 3. Spikes as measurements
By measuring the head's dynamical state each time a particular neuron fired during broad-band head angular velocity noise stimulation, we computed conditional probability density functions for head state at spike times (Figure 1). The state variables are head angular velocity and head angular acceleration. The conditional pdf for a particular neuron quantifies likely head states at the firing time.

The conditional distributions have smaller entropy (ie. are more localized in the state space) than the distribution of head states. This means that observing a single spike provides information about head state. The amount of information is quantified in bits, the entropy difference between the head state pdf and the conditional head state pdf, in base 2. One bit corresponds to a reduction in the area of the distribution (or in the area of a confidence ellipsoid for head state) by a factor of two. We estimated, using spike trains from fitted models, that a single spike in a bullfrog semicircular canal afferent neuron conveys approximately half a bit of information about head state.

The conditional distribution allows us to represent a spike explicitly as a state measurement. The distributions are approximately bivariate gaussian, and for a given neuron can be accurately fitted using a mean vector $x_k$ and a 2x2 covariance matrix $\Sigma_k$. This shows explicitly that the information provided by a spike is identical to the information provided by a conventional vector measurement *x* with an associated error covariance $\Sigma$.
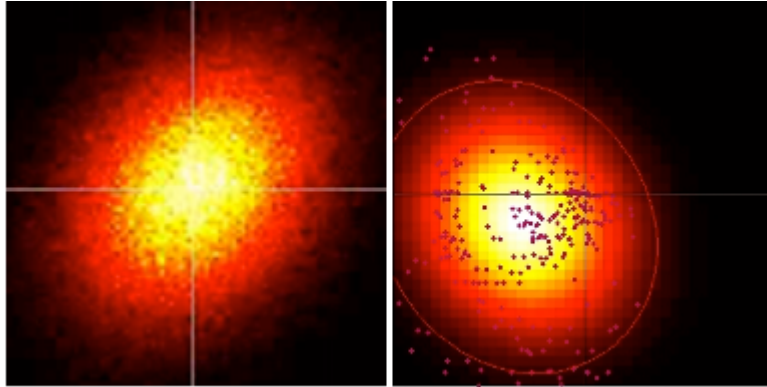


Figure 1: Distribution of head states (left) and conditional distribution of head states (right) at spike times for a bullfrog horizontal semicircular canal afferent neuron.

There are some important differences between spike measurements and conventional measurements. Spike measurements are asynchronous, $y_k = x_k + v_k$, with $t_k = k$th spike time. Conventional measurements are usually either continuous, [ ~~✗~~ ], or discrete and made at regular intervals, $y_k = x_k + v_k$ with $t_k = k\Delta t$. Spike measurements from a given neuron always provide the same vector. Conventional measurements change systematically through time, except in the special case of observing a static system. Spike measurements always have the same error covariance. Conventional measurements may have time-varying error covariance, $\Sigma = \text{cov}(v)$.

## 4. Neural Computation based on Spike Measurements
Measuring devices that always report the same measurement, with large, fixed random error, would seem to be of limited utility. But spike measurements can be seen as dynamical equivalents to receptive fields in spatial coding by sensory neurons. Although they only report very localized stimuli, and then ambiguously and unreliably, arrays of such devices can clearly provide very accurate sensory information.

In conventional multivariate dynamical systems theory, state space converts dynamics into geometry, allowing dynamical problems to be attacked using algebraic matrix-vector methods. Identifying spikes with vector measurements does this and more. It not only embeds spikes in existing dynamical systems theory, it makes it possible to extend that

theory to encompass topological computation in neural systems. That is, computation implemented by patterns of connectivity among populations of specialized computing elements. We illustrate this with two very simple models of central computation.

There is compelling evidence that the cerebellum plays a role in dynamical state estimation and prediction for perceiving and controlling movement [3]. The vestibular nuclei, central projection sites of vestibular sense data, are displaced cerebellar nuclei and provide a prototypical model system for cerebellar computation. We consider the simplest state estimation problem in the current context, that of combining vestibular measurements to estimate head dynamical state from sense data.

First, consider the situation where several spikes arrive simultaneously, and we have no prior knowledge of head state. This is an ordinary static estimation problem, and the solution is to form a weighted sum of the measurements [ ✕ ] , using the covariance matrices to assign weights according to the reliability of each datum. Note that this is a subtle generalization of the "population firing rate vector" in which we quantify the specificity of individual neural responses when counting "votes" in a computation, and express the result as a vector in state space rather than in "firing rate" space.

Next consider the situation where we have an existing estimate $\hat{x}(t)$ with error covariance $\Sigma(t)$, based on spike measurements up to time $t$. Then neuron $k$ fires at time $t'$ bringing the measurement $y_k = x_k + v_k$ with $\Sigma_k = \text{cov}(v)$. The optimal updating rule can be obtained by generalizing the Kalman filter theorem. Propagate $\hat{x}(t)$ and $\Sigma(t)$ to time $t'$ and then form a weighted sum of $\hat{x}(t)$ and $y_k$ with weights determined by $\Sigma(t)$ and $\Sigma_k$.

More generally, spikes from various sources carrying information about head movements must be projected into the appropriate state space and weighted according to their reliability. Our simple examples will demonstrate how computations using spikes can be analyzed, and models of spiking systems can be constructed, using the rigor and power of dynamical systems theory.

**References**
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