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

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Abstract
We recorded spike trains from bullfrog semicircular canal afferent neurons during broad-band rotational stimulation. Conditional probability density functions for head state at spike times have smaller entropy than the unconditional distribution of head states, showing that individual spikes transmit on average about 0.1-1 bits of information about head state. This shows that it is possible to treat single spikes as measurements or assertions about head state. Building on this observation, we show how single spikes may be treated as operands in neural computation.

1. Introduction
About 1200 neurons transmit information from each semicircular canal to the brain of the bullfrog, *Rana catesbeiana*. There is a wide variety of response properties, with varying phase and sensitivity during rotation at different frequencies [1]. The large number and behavioral diversity of these neurons is curious, since each canal measures just one degree of freedom of head motion. Why does nature run hundreds of signal leads from a device that, from a conventional engineering perspective, would seem to require just one?

This question has usually been answered by suggesting that many neurons are required because they are individually very noisy and may fail. But measurement accuracy improves only with the square root of sample size, and simple cost-benefit analysis then makes it difficult to believe that it could be worthwhile to use thousands of very bad measuring devices in preference to a much smaller number of slightly better ones. An alternative suggestion is that individual semicircular canal afferent neurons may transmit highly specific information about head movement patterns [2, 3]. This view is supported by the observation that behavioural differences between these neurons are highly reproducible [1]. This would not be expected if the differences were due to measurement noise.

Our goal in this paper is to present a new way to characterize the response specificity of vestibular semicircular canal afferent neurons, and show how it leads naturally to models of neural computation using spikes as operands.

2. Single spikes contain stimulus information

Calculating the instantaneous firing rate of a spike train involves a free parameter that corresponds to the smoothing window diameter or filtering bandwidth [4]. This parameter can be estimated by cross-validation using information gain per spike [5],

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

where $s_k = 1$ if there is a spike in the kth sample period and zero otherwise; r_k is the estimated instantaneous 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 by the instantaneous rate estimate than by average firing rate. The model with maximum information gain is the maximum likelihood model, and so I_S provides a general criterion for comparing and selecting models of spiking neurons [5].

We subjected bullfrogs to broad-band (0.05-2Hz) rotational velocity white noise stimulus and recorded spike trains from semicircular canal afferent neurons (Figure 1).
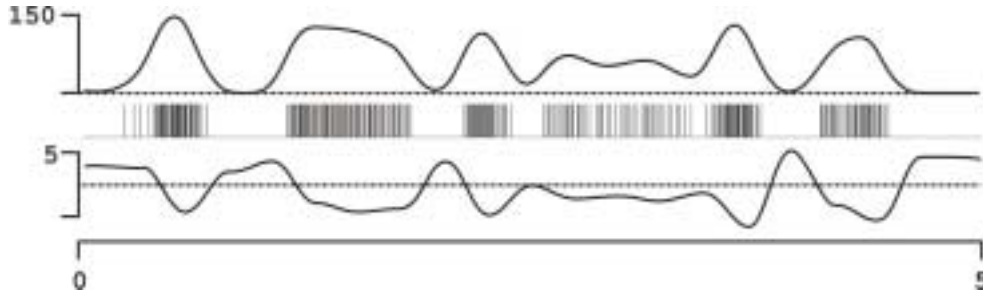

Figure 1: Five second segment of a recording of a horizontal semicircular canal afferent neuron responding to a broad-band stimulus. The lower trace shows turntable (head) angular velocity, the middle trace shows spikes, the upper trace shows instantaneous spike rate obtained by gaussian smoothing [4].

On average the optimal bandwidth for these neurons was 1.6 times their spontaneous firing rate (range 0.52–2.6). This means that these neurons have highly reproducible spike timing patterns, and optimal smoothing windows for rate estimation typically contain about 1 spike. Correspondingly, these neurons have information gains of 0.07-0.85 bits per spike, averaging 0.40 bits, indicating that individual neurons transmit significant amounts of information on a timescale corresponding to arrival times of individual spikes.

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3. Extracting information from single spikes

From a systems-theoretic point of view the vestibular system provides the brain with dynamical state variables of the head. Horizontal canal afferent neurons provide information about the state variables related to rotation about the canal axis. We recorded the value of these state variables at spike times of individual neurons during head rotation, to obtain two-dimensional frequency histograms showing the conditional distribution of head state at spike times (Figure 2).
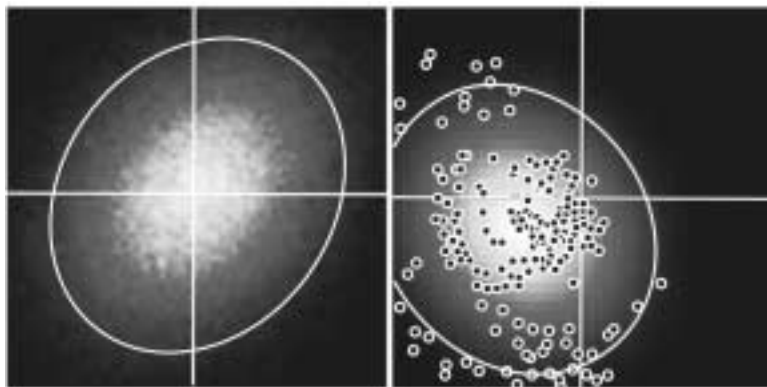

Figure 2: Distribution of head states (left) and conditional distribution of head states at spike times (right) for a bullfrog horizontal semicircular canal afferent neuron. The 95% confidence ellipsoid is shown for each distribution. Head states at spike times are indicated on the conditional distribution. The conditional distribution quantifies what can be deduced about head state when a spike is observed.

The conditional distributions are more localized in the state space than the unconditional distribution of head states, implying that single spikes provide information about head state. The amount of information can be quantified in bits, equal to the entropy difference between conditional and the unconditional head state probability density functions in base 2. We find that on average a single spike in a bullfrog semicircular canal afferent neuron transmits about half a bit of information about head state.

4. Modeling neural computation with single spikes

The frequency histograms of head state at spike times are approximately bivariate gaussian distributions, and can be accurately fitted using a mean vector x_k and a 2x2 covariance matrix Σ_k. This means that we can represent a single spike as a measurement that is formally identical to a conventional discrete noisy measurement of a vector quantity, $y_k = x_k + v_k$, where $\Sigma_k = \text{cov}(v_k)$. Unlike conventional measurements, spike measurements from a given measuring device (sensory neuron) always report the same value with the same error. Also unlike conventional measurements, the rate at which measurements are made varies depending on the state of the observed system. Measurements are more likely to be made when the stimulus state is near the spike measurement mean.

Measuring devices that repeatedly report the same measurement at arbitrary times, with large, fixed random error, would seem to be of limited utility. But these measurements can be thought of as receptive fields in state space. As is well known from other sensory systems, notably vision and tactile senses, receptive fields can be regarded as radial basis functions (RBFs), providing a convenient and flexible foundation for modeling distributed computation in neural systems. For example, hyperacuity – the ability to discriminate stimuli that are much smaller than sensory receptive field sizes – is easy to understand and model using RBFs. More significantly, modeling sensory spikes as probability density functions in state space makes it possible to understand how the nervous system could update central representations and motor responses instantaneously when new information arrives in the form of a sensory spike.

For example, consider the problem of estimating head dynamical state from vestibular sense data. The vertebrate nervous system represents head state in the vestibular nuclei, which are the central targets of vestibular (and other head-state related) sense data. We assume that knowledge of head state is represented in a distributed form by a population of spikes in these nuclei. As these spikes move along axons in the vestibular nuclei, we think of them as a cloud of points moving through a map of head state space[1]. The reliability of knowledge is reflected in the distribution of the population over the map; more points, or more compact distribution of points, means more certainty about head state.

In the absence of sense data the central representation will become increasingly unreliable, and this will be reflected both in the diffusion of spikes over the map and in the loss of spikes as they fail to propagate across synapses. Information in sensory spikes can be captured both by facilitating central neurons so that existing spikes are regenerated at synapses, and by injecting new spikes into the map. The difficulty is in determining which central spikes should be allowed to die, and where and how many new spikes should be injected when a measurement is made. The solution to this problem depends on the relative reliability of the central representation (i.e. how points are distributed over the map) and the incoming measurement. We hypothesize that the shaping of vestibular nucleus sensitivity to capture the information present in sensory spikes is the function of cerebellar cortex [6]. We are currently developing a computational model of how this could be implemented in the brain.

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[1] Probably there are multiple maps, a technicality that we ignore for the time being.

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