Spikes are the Operands of Neural Computation

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Abstract: Individual spikes of sensory neurons can be treated as instantaneous measurements. Conventional numerical methods, such as the Kalman filter, can be implemented in asynchronous forms that use these measurements directly. But clearly the brain does not compute this way. The key to understanding how neurons may compute using individual spikes as operands is to realize that – metaphorically speaking - a spike is a particle, not an event.

1. Coding in the vestibular nerve

Larry Hoffman (lfh@ucla.edu) and I have been studying how vestibular sensory neurons encode information about head movements. We recorded spikes of neurons projecting from the semicircular canals of the vestibular system of the bullfrog, Rana catesbeiana, during angular accelerations. These neurons fire spontaneously, and increase and decrease their firing rate as the head turns back and forth around the canal axis (Fig 1). They would seem to epitomize the paradigm that sensory neurons encode the amplitude of a stimulus in their firing rate.

About 1100 sensory neurons project from each semicircular canal into the bullfrog’s brain [1]. There are two canals in each plane, providing well over two thousand neurons to monitor just one degree of freedom of head movement. In bullfrogs, as in all species studied, there is surprisingly wide variation in the response properties among neurons in this population (ibid.). The initial interpretation of these observations was that the firing rate of an individual neuron provides very noisy sense data, and that many such measurements are required to obtain accurate information.

We were skeptical about this view. While there is large variation in response properties, individual neurons respond consistently on repeated trials using the same stimulus. This suggests that the variation may be individual response specificity rather than noise [2]. There are many neurons within the population whose firing rate – adjusted for spontaneous firing rate and sensitivity - does very accurately reflect the head angular velocity. So this sensory system would seem to have the capacity to encode angular velocity in firing rate with relatively little noise, using far fewer than 2000 sensory neurons; but it apparently chooses not to. Finally, it is clear that here, and in general, sensory signals don’t get “decoded” by averaging when they get into the brain. Vestibular sensory neurons fan out onto a much larger population of secondary vestibular neurons as they enter the brain. Nerves and brains evidently use some kind of spatially distributed representation(s) of movement.

How might spike trains in the vestibular nerve represent movement? From an engineering - control theory point of view it is obvious what the brain wants to know about head movements: The dynamical state variables. We might argue about whether the brain needs to explicitly represent the head state variables in order to do things like, for example, correctly interpret spatial information provided by sensor arrays attached to the head. Or we could simply look and see if it does, which is what Larry and I did.

Figure 1: Firing rate of a bullfrog vestibular semicircular canal sensory neuron during broad-band (0.05-2Hz) angular velocity stimulus [4]. The photograph is of the vestibular labyrinth of the New Zealand swell shark, courtesy of Prof. John Montgomery.
2. Sensory spikes are state measurements

We used broad-band angular velocity white noise stimuli (0.05-2Hz; cf figure 1) and recorded spike times of semicircular canal sensory neurons with 1ms resolution. Then we looked at the distribution of head states at spike times for each neuron. In practice this means building a histogram to estimate the probability that the head will be in a given region of the state space when the neuron fires. We used a two-dimensional state space corresponding to rotation around a single canal axis.

We found that the distribution of head states at spike times tends to be more localized than the overall or prior distribution of head states during the stimulus. The conditional distribution also tends to be offset from the mean of the prior (figure 2). This means that a single spike carries information – albeit not much – about head state.

![Figure 2](image.png)

**Figure 2**: Conditional probability densities of head state at spike times for eight bullfrog semicircular canal afferent neurons subjected to broad-band angular velocity stimulus. Individual neurons have “preferred regions” in the state space [3].

The conditional probability densities of head states at spikes times (figure 2) are approximately bivariate Gaussian. This means that, at least to some reasonable approximation, we can model a single spike as a conventional state measurement, $x_i(t_{ik}) = \bar{x}_i + e_i$, where $x_i(t_{ik})$ is the measurement provided by the $k$th spike of the $i$th neuron. The measurement consists of a mean value $\bar{x}_i$ plus an error $e_i$ given by the conditional pdf.

Having sensors that always report the same measurement with the same, fairly large, error would not seem to be very useful. However, if there are many such neurons, with preferred states scattered widely over the space of possible states, it is straightforward to extract accurate state estimates using a minor modification the standard Kalman filter (KF) algorithm. The standard KF assumes that measurements are made at regular intervals $\Delta t$, but it is easy to adjust parameters at spike arrival times so that the KF equations remain valid using asynchronous discrete measurements provided by spikes [4]. This shows that it is possible to treat spikes as measurements, and carry out useful computations with them. However, the computations are neither elegant nor plausibly neuromorphic.

3. Action potentials are particles

The key to unlocking how brains may compute with spikes may be the realization that the “event-like” character of spikes is an artifact, caused by the way that spikes are observed by neuroscientists. Spikes are local reversals of neural membrane potential that propagate along thin axons to their targets. Neurophysiologists observe them using fine-tipped microelectrodes that “see” them momentarily as they pass by (Figure 3). Often in the laboratory the microelectrode signal is amplified and fed into a loudspeaker, providing an audible “click” to accompany the visible “blip” on the oscilloscope screen, compounding the illusion that a spike is a localized event. It is more realistic to think of spikes as “virtual particles” that move within and between “maps” in the nervous system [5].

4. Neural computing with particles

How does the virtual particle model of spikes help to solve the problem of how real, biological neural networks can compute with spikes? It turns out that “particles” are natural operands
Figure 3: A spike is a local reversal of potential that travels over the neuronal membrane. Spikes are observed using spatially localized sensors that detect an event – the potential change caused by the spike as it passes by the tip of the electrode. (Original neuron image from http://www2.uni-jena.de/biologie)

in the Monte-Carlo approach to dynamical filtering and state estimation problems. This approach is becoming popular [6] as cheap computers acquire the capacity to perform massively parallel dynamical simulations.

To illustrate the particle filter approach, and the kind of computational operations that are required, consider the problem of estimating the state of a one degree-of-freedom pendulum, perturbed by white noise and observed with Gaussian error. For small angles this is a mildly nonlinear system, and both the ordinary and the usual extended KF would be close to optimal for this problem.

Figure 4 shows ten simulations of the pendulum trajectory from an initial state distribution at time \( t_0 \) up to time \( t_1 \). This is illustrated using ‘particles’ drawn on a map of the pendulum’s state space. With a sufficiently large sample size the conditional state distribution at \( t_1 \) given the distribution at \( t_0 \) can be estimated easily and accurately, by looking at the particle distribution at simulation time \( t_1 \). Indeed, the particle distribution is an estimate of the state distribution. Now suppose a new measurement is available at \( t_1 \). In the simplest version of a particle filter, we simply inject a cloud of particles whose distribution corresponds to the new measurement, and carry on simulating.

Figure 4: Ten simulated state-space trajectories (white “particles”) of pendulum (inset) perturbed by Gaussian noise. From initial distribution (left) clockwise to the final distribution at t=1 second. The red trace shows the trajectory of an unperturbed pendulum starting at the mean of the initial state distribution. The total energy (Hamiltonian) of the pendulum and its level curves are shown. Horizontal axis is angle from vertical, \(-\pi < \theta < \pi\); vertical axis is angular velocity.

Injecting a new cloud of particles for each new measurement is fine in theory, but in practice it requires more hardware or memory each time. Bullfrog’s semicircular canals each make tens of thousands of measurements each second; ours make orders of magnitude more. Older particles are less likely to be near the true state, so intuitively we should “condense” the cloud as new particles are injected.

Condensation can be done in different ways, with varying degrees of sophistication [5]. The simplest rule is to create a new standard-sized cloud at time \( t_1 \), whose distribution matches the overall distribution of particles propagated from \( t_0 \) and particles injected at \( t_1 \).

This rule mimics the Kalman filter in a simple-minded way. It gives only an approximation, but our experience confirms reports e.g. [7] that errors due to this approximation are negligible in comparison to other sources of error in state
estimation, even with only a few hundred particles. Neural systems could implement huge numbers of virtual particles.

Particle filters have none of the theoretical restrictions of the Kalman filter – target linearity, Gaussian errors and disturbances. Their downside is that they are neither fast nor compact when implemented using conventional computers. On the other hand, particle filters can be implemented very easily and efficiently using parallel hardware. Most importantly in the current context, they can be implemented using only simple “neuron-like” operators, such as time delays and sums.

Figure 5: Basic vestibulo-cerebellar circuit. Cerebellar Purkinje cells inhibit brainstem neurons receiving signals from the vestibular apparatus.

5. A particle filter model of cerebellum

The neural architecture required to implement a particle filter for head state estimation would seem to resemble the architecture of the vestibulo-cerebellum (figure 5). In our model (Paulin and Assad, unpublished) vestibular nucleus neurons form a head state map, and are connected so that spikes spread over the map mimicking the dynamics and statistics of head movement. Sensory neurons are coupled to this map so that when they fire they inject clouds of spikes whose distribution matches the conditional distribution of head states at firing times (Figure 6).

Overlying the state map, receiving signals from it and projecting back to it, the cerebellar cortex acts as a neural condenser. To a first approximation, the cerebellar cortex simply provides inhibitory feedback that stops the particle cloud from saturating the map. We are developing a subtler model, in which cerebellar cortical inhibition maintains Bayesian optimality. It annihilates particles so that the entropy (“size”) of the particle cloud in the brain corresponds to the information content of received sense data.

This particle filter model of the vestibulo-cerebellar system is testable, and may help to understand the wider role of the cerebellum in motor control, perception and cognition [8, 9].

Figure 6: “Golgi stained” vestibular nucleus neurons in a computational neural particle filter model of optimal head state estimation in the vestibulo-cerebellar system (Paulin and Assad, unpublished). Axon pathways and synaptic weights are constructed to match the statistics and dynamics of the target (a pendulum in our current model).


