Functional Organization Of The Vestibulo-Ocular Reflex

A Simulation study of the contribution of stochasticity and lateral inhibition to reflex function.

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Introduction

The Vestibulo-Ocular Reflex (VOR) is responsible for moving the eyes in response to head movement so as to stabilize the image on the retina. This is necessary to maintain clear visual perception while walking.

The basic functional mechanism of the horizontal VOR is illustrated in figure 1. Input is a bipolar, differential head velocity signal from the semicircular canals to the medial vestibular nuclei (MVN). The network must induce the eyes to rotate exactly in compensation.

This reflex has two cardinal features: The spontaneous noisy manner in which MVN cells fire[1] and the commissural inhibition (CI) link between the MVNs.

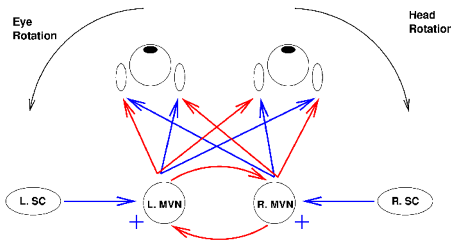

Figure 1 – Schematic of VOR function
Blue: Excitatory, Red: Inhibitory

Fourier analysis of VOR action in man indicates that it must compensate for head frequencies of up to 20Hz. How can it relay input frequencies which are large compared to the static rate of MVN cells?

Theoretical studies[2] of signal transmission in neural populations show this is possible for rate coding across a population of asynchronous neurons. However, populations also synchronize in response to strong high frequency inputs. This problem is particularly acute in the VOR because of differential amplification by the CI link. Could the noisy MVN activity enable the reflex by maintaining asynchrony?

With these questions in mind, we developed a leaky integrate and fire (LIF) model of the core bilateral VOR to investigate the functional significance of the cardinal features of commissural inhibition and spontaneous noisy activity.

Methods

We consider the integrate and fire model

$$\tau_m \frac{dV_i(t)}{dt} = -V_i(t) + R_m(I(t) + P_i + \epsilon(t)) \qquad \epsilon(t) = N(0, \sigma_1)$$

for which we have special cases where $P_i = N(m, \sigma_2)$

- $\sigma_1, \sigma_2 = 0$ — No stochasticity
- $\sigma_1 > 0, \sigma_2 = 0$ — Diffusive synaptic noise, ε
- $\sigma_1 = 0, \sigma_2 > 0$ — Heterogeneous spontaneity, P_i
- $\sigma_1, \sigma_2 > 0$ — Heterogeneity and noise

The network's task was to replicate a driving input, I(t). Assessment was based on the response fidelity, gain and phase lag as we varied input frequency and amplitude to physiological extremes.

Results

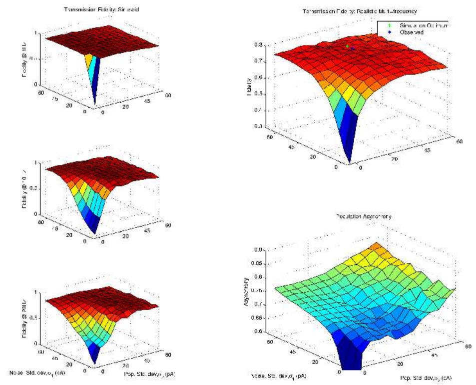

Figure 2 – Optimum Noise Band

Figure 2 (left) illustrates output fidelity as a function of noise strength and input frequency. Figure 2 (right) illustrates network fidelity and asynchrony for realistic multi-frequency input. The purely deterministic cases fail completely, and performance deteriorates at very high noise levels. Between these extremes is a band of noise induced high fidelity. Interestingly, biological levels of population variability were found to be well in line with the simulation optimum. Similar results were observed for output gain and phase.

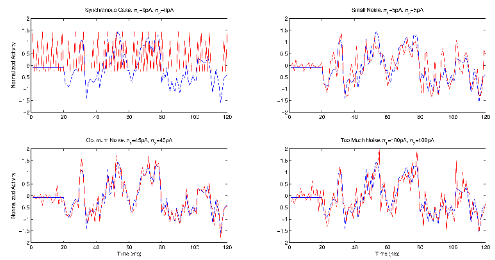

Figure 3 – Network Transmission Fidelity
Blue – Input, Red - Output

Figure 3 shows detailed samples of network activity. Too little noise fails to prevent population synchrony (top), too much noise reduces fidelity (bottom right). The best trade-off (at the highlighted point from figure 2) between the benefits of asynchrony and the disruptive effects of noise is shown in the lower left.

Discussion

From this work we conclude that stochasticity in the form of diffusive noise input and or population heterogeneity is crucial in maintaining VOR performance in demanding real world regimes.

This may well explain how it is that the domain of animal VOR performance does indeed extend beyond that which is predicted by previous experimental and theoretical single neuron studies.

Using computer simulation to relate theoretical work to the specific function of a real world neural system, this investigation provides insight into the functional significance of cardinal VOR features.

References

1. M Serafin et al. Medial vestibular nucleus in the guinea pig I. Intrinsic membrane properties in brainstem slices. *Experimental Brain Research*, 84:417-425, 1991
2. Bruce W. Knight. Dynamics of Encoding in a Population of Neurons. *J. Gen Physiol.*, 59(6):903-911, 1972.

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