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Poisson or Not Poisson: Differences in Spike Train Statistics between Parietal Cortical Areas

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The variability of neuronal responses is proportional to the mean in many brain areas, which suggests that neural responses might follow a Poisson distribution. In this issue of *Neuron*, Maimon and Assad document a surprising violation of Poisson firing. Specifically, they show that there are differences in the amount of periodic structure in spike trains across cortical areas, with multimodal sensory areas being more regular than visual areas.

Since its earliest descriptions (Tolhurst et al., 1981; Werner and Mountcastle, 1965) the proportional relationship between the mean and variance of neural responses has been taken as one of the fundamental facts of neural coding, relevant almost anywhere in the brain. Based upon this fact, it has often been assumed that neuronal firing rates are reasonably well described as Poisson. If spike times were distributed as a Poisson process, the time of a spike would not depend on when the previous spike occurred, and the interspike interval (ISI) distribution would be exponential. In this issue of *Neuron*, Maimon and Assad (2009) show that, while this assumption is reasonable for areas MT and MST, it breaks down for areas 5 and LIP of parietal cortex. The Poisson assumption has broad implications for information coding, computation, and ultimately, behavior.

While neural responses are often assumed to be approximately Poisson, several features of real neural responses violate the assumptions of this model, and even the mean-variance relationship has been challenged. While this relationship has been shown to hold almost ubiquitously under certain conditions, there are also many conditions under which it breaks down. For example, spike counts in many tasks are measured using relatively large windows, on the order of hundreds of milliseconds or a few seconds, and in this case the mean-variance relation often holds well. The mean-variance relationship does not hold well, however, when using smaller windows for estimating spike counts (Amarasingham et al., 2006; Averbeck and Lee, 2003; de Ruyter van Steveninck et al., 1997; Kara et al., 2000). Thus, whether or not neurons respond in a Poisson-like manner depends on the timescale under consideration. This raises the question of which timescales are relevant in the brain. Relatively flat mean-variance relationships can be seen at less than 100 ms, however, and perceptual and motor systems are likely operating at timescales smaller than this. Other studies have shown that removing behavioral variability (Gur et al., 1997) or using threshold sensory stimulation (DeWeese et al., 2003) can also substantially decrease the mean-variance relation.

In addition to reliance on bin sizes, three features of neural responses have been shown to contribute to decreasing variability, including the refractory period (Kara et al., 2000), bursting (Barbieri et al., 2001), and temporal correlations in neural responses on longer timescales (Averbeck and Lee, 2003). All of these features can be modeled by including history dependence in spike train prediction. This is, however, a fundamentally non-Poisson feature, as the spike times in a Poisson process would not depend on the history of prior spikes.

Maimon and Assad report another fundamental deviation of neural responses from Poisson and they further show that this feature differs across brain areas. They find that the ISI distributions are more periodic or pulsed in areas LIP and 5 (Figure 1A; blue line) than they are in areas MT and MST (Figure 1A; red line). This increased regularity also leads to a decrease in the variance of the response for the corresponding mean (Figure 1B; blue dots for regular, red dots for exponential ISIs). The fact that this deviation systematically varies across cortical areas suggests a fundamental difference in the way these areas process information and in the organization of the local network or the response properties of the individual neurons. There are a number of strengths to this study, including a series of analyses which show that that this effect does not come about because of bursting, long-refractory periods, the bin size used for the analysis, or microsaccades made by the animals in the task. Furthermore, because the data were collected in an awake, behaving monkey, the effects cannot be ascribed to anesthesia. Thus, this seems to be a fundamental feature of the neural responses that cannot be easily ascribed to previously reported response properties.

The implications of this result and related results seen in frontal motor areas (Shinomoto et al., 2003) for coding, computation, and behavior remain to be elucidated. The decrease in variance for a similar mean response would appear to imply increased information coding, because of the increased signal to noise ratio. However, the authors did not find a relation between the regularity of the spike discharge and the coding capacity of individual neurons. Furthermore, information coding in populations depends on other factors that may be independent of the pulsed coding, specifically correlations between neurons in the population (Averbeck et al., 2006), and as such, there is no necessary link between the regularity of the coding in single neurons and the information coded at the population level.

Of additional interest for coding is the fact that the single neuron variance decreases in this study as one progresses from sensory to higher-order sensory-motor areas. A previous study in the early visual system has shown increased variability in neural responses as one moves from the sensory periphery to the cortex (Kara et al., 2000), which is consistent with the idea that there is noise added at each stage of sensory processing. The results of the current study seem to suggest a decrease in noise with additional processing steps. While this is interesting, it is not possible to actually increase information coding with additional processing, and as such information cannot increase as one progresses through stages of neural processing. Thus, the increased regularity and decreased variability in the single-cell responses has to be compensated by other factors that decrease or at best maintain information.

A second possible implication relates to recent theoretical models of decision-making processes in parietal cortex that rely on Poisson-like variability (Beck et al., 2008; Ma et al., 2006). Specifically, it has been shown that integrating spikes from neurons with Poisson-like variability can lead to Bayes optimal inference. The results of Maimon and Assad would seem to suggest that the basic assumptions of this decision-making model do not hold well in areas LIP and 5. However, the model has been applied to LIP integration of MT neural responses and Maimon and Assad suggest that the MT neurons are more Poisson-like than the LIP neurons. Specifically, the linear mean-variance relation holds best in MT/MST. Furthermore, the theory is somewhat robust to deviations from Poisson-like responses, although it is not clear how robust it is. Thus, it is possible that the increased regularity observed in areas LIP/5 is related to downstream inference processes carried out on MT/MST responses, as the regularity may affect subsequent inference.

Maimon and Assad have described a very interesting difference in the regularity of neural responses across brain areas. Perhaps now that we have been exposed to these differences, we will begin seeing them in more data sets and trying to understand what they mean.

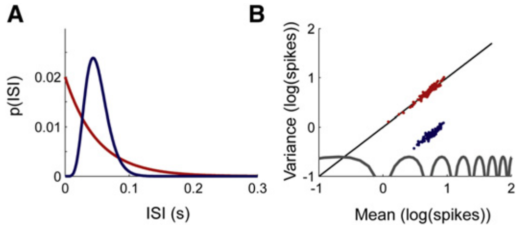

Figure 1. Interspike Interval Distributions and Mean-Variance Relations for Exponentially Distributed and Regular Neurons

(A) Example gamma distributed interspike intervals for exponentially distributed (Poisson-like; red) and nonexponentially distributed (regular; blue) neurons. Neurons in areas MT/MST are approximately exponential (minus the refractory period) and neurons in areas LIP/5 are more regular.

(B) Mean-variance relations for example populations of 100 neurons with exponential (red) or nonexponential (blue) ISI distributions and variable firing rates. The gray curves indicate the minimum variance possible given the discrete nature of spikes.

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