TEMPORAL UNCERTAINTY IN READING THE NEURAL CODE (MULTIPLICATIVE NOISE)

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1. Introduction

Noise places limits on the performance of machines. It limits the resolution of sensory transduction, the precision of motor output, and the rate of information transfer of channels. Nervous systems are not exempt from these constraints. The noise limits of human sensory and motor performance have been extremely well studied for more than a century with remarkably consistent results that have become accepted as empirical ‘laws’ such as Weber’s law and Stevens’ law for sensory/ perceptual processes, and Fitt’s law for motor behaviour. The vast amount of data underpinning these laws have been gathered from many sensory and motor modalities and show that performance is limited by signal-dependent noise, where specifically the standard deviation of performance increases with the performance mean, which we call ‘proportional noise’ (PN). Also, many aspects of motor dynamics can be explained as optimal in the presence of PN (Harris & Wolpert, 1998).

It is inescapable that over a wide operating range, human performance is limited by PN. What is the origin of this noise, and why is it so ubiquitous? From an evolutionary perspective, PN might reflect either some highly desirable (‘deliberate’) state of affairs, or some unavoidable constraint of biological performance. At present we have no theoretic reasons for the benefit of PN, so we explore the possibility that PN reflects some ultimate constraint. Here, we confine our arguments to motor systems.

Could PN arise from the inherent stochastic properties of neuronal firing patterns? When signals are transmitted by action potentials, it is common to model noise as a renewal process (RP). Inter-spike intervals (ISIs) are assumed to be identical independent random variables, which leads to the well-known asymptotic statistical relationships of renewal noise (RN) (i.e. over the infinite time horizon). The most important is that the variance of spike rate is proportional to the of mean spike rate, regardless of the ISI distribution. Although RN is a form of signal dependent noise, it is quite distinct from PN. Even with local dependence between adjacent ISIs, the asymptotic statistics are still renewal-like. In practice it is remarkably difficult to combine RPs without yielding RN statistics - the renewal trap !

A serious objection to renewal theorems is that they are asymptotic; that is, they are based on expectations of firing rate moments over the infinite time horizon. Brains make decisions in finite time and can make very fast behaviours -- indeed, one could argue that speed of response is evolutionary important. What are the statistics of finite renewal processes - do they behave radically different from asymptotic processes? Finite time horizons require time to be measured, and since brains do not have crystal clocks, there must be some degree of uncertainty in measuring time. What is the effect of time uncertainty?

2. Results

Finite Renewal Processes with Deterministic Time

The theory of renewal processes can be applied to moments of spike count in the finite interval (0,*T*) (Cox & Miller, 1965; Karlin & Taylor, 1975) (which we call 'finite renewal processes'). Denote the number of spikes in the *deterministic* interval (0,*T*) by the random variable *N*. Denoting $F = 1/T$, then the mean and variance of spike rate, $\overline{R}$, in the interval (0,*T*) is:

$$\overline{R} = \mathrm{E}\{NF\} = \overline{N}F \quad \text{and} \quad \mathrm{V}\{R\} = V\{N\}F^2$$

where E{.} = mean, V{.} = variance. We solve these equations for renewal processes for various ISI distributions, either from closed forms (where possible) or from numerical analysis, and show that variance tends to be a compressive function of the mean, rather than accelerative as expected for PN. For large *T*, variance becomes a linear function of mean rate with a slope and intercept depending on the underlying ISI distribution. Only for the exponential ISI distribution (Poisson process) is the intercept zero. Thus, in general RPs over finite time do not behave like asymptotic RPs. A finite RP cannot lead to PN by itself. In order to generate PN, the form of the ISI distribution would need to change systematically with its mean.

….with Time Uncertainty

It is implicit that the time signature of a spike requires some measure of time. We now assume that there is variability in the estimation of time intervals. This means that when spike rate is estimated, *T* is also a random variable. Then the mean and variance of spike rate are:

$$\mathrm{E}\{R\} = \mathrm{E}\{NF\} = \overline{N}\,\overline{F} + \mathrm{C}\{N,F\} \tag{1}$$

$$\begin{aligned}\mathrm{V}\{R\} = \mathrm{V}\{NF\} &= \mathrm{V}\{N\}.\overline{F}^2 + \overline{N}^2.\mathrm{V}\{F\} \\ &+ \mathrm{V}\{N\}\mathrm{V}\{F\} + \mathrm{C}\{N^2,F^2\} - \mathrm{C}\{N,F\}^2 - 2\overline{N}\,\mathrm{C}\{N,F\}\overline{F}\end{aligned} \tag{2}$$

where C{.,.} = covariance. The importance of eqn.2 lies in the second r.h.s. term, which increases with the square of the mean rate $\overline{N}^2$, that is, it is PN.

For the sake of illustration assume that *N* and *F* are independent with small coefficients of variability, and consider the special case where *N* is a renewal process with a Fano number *k*, then

$$\mathrm{V}\{R\} \approx k\overline{N}\,\overline{F}^2 + \overline{N}^2 V\{F\} \tag{3}$$

For very low firing rates, variance is dominated by the first term indicating RN, but as firing rate increases the variance becomes rapidly dominated by the second term, which is PN. Of course *F* and *N* are not generally independent, which leads to the complications in eqn.2.

Stochastic Approach

The brain tends to measure time via leaky integrators. Incoming action potentials are integrated over time and leaked away ('shot noise'). Here we consider a simple linear system in which the input is a RP (a stochastic signal) , $u(t)$, and the decay is defined by the impulse response function, $p(t)$. The key assumption is that $p(t)$ is stochastic.

Consider the transfer of spikes to muscle force. The output (muscle force) is $y(t) = \int_0^t p(t-s)u(s)ds$, with a mean square (autocorrelation R) given by $R_y(t,t) = \int_0^t \int_0^t R_p[(t-s),(t-r)]R_u(s,r)dsdr$ assuming p and u are independent. Converting to covariances and assuming they are small compared to their means (ie. we ignore products of covariances):

$$V\{y(t)\} \approx \int_0^t \int_0^t C_p\{t-s,t-r\}\overline{u}(r)\overline{u}(s)dsdr + \int_0^t \int_0^t C_u\{s,r\}\overline{p}(t-s)\overline{p}(t-r)dsdr . \qquad (4)$$

Again, we see the two components: the first r.h.s. terms of order of the square of $\overline{u}$ (ie. PN) and the second r.h.s. term involving the RP covariance C_u, which proportional to $\overline{u}$ (ie. RN). An explicit solution of eqn.4 is difficult; therefore, we next considered a concrete example by numerical analysis.

A Muscle with a First-order Leaky Integrator Model

We considered an idealised simple 1^{st}-order linear motor system in which each incoming action potential generated a muscle force impulse with a time-course given by a decaying exponential (ie. 'shot-noise'). We used a discrete time approximation: $y_{i+1} = (a + x_i)y_i + u_i$ where a was a constant, $u_i = 0$ or 1 if a spike was present, and x_i was a zero mean Gaussian random variable.

When the input was a deterministic (a periodic spike pattern), the steady-state output force variance was related linearly to the square of the mean output force, consistent with PN. When the input was stochastic (modelled by a gamma ISI distribution), the output variance was a mixture of RN and PN depending on the ISI coefficient of variability. Thus, RN on the input would translate to RN on the output and could swamp the PN. These results confirmed the general principle embodied in eqn. 3 and eqn.4.

3. Discussion

Motor Behaviour

The variance of a finite renewal process is a compressive function of the mean, and does not yield PN. To obtain PN it would be necessary for the ISI distribution to be a systematic function of the mean firing rate. We cannot exclude this complicated possibility, but a more parsimonious explanation is that PN arises from fluctuations in time estimation. For muscles, time uncertainty can be viewed as a form of 'multiplicative noise' with variability in the gain (transfer function).

The RN component of force variance can be reduced by lowering the variance of the input σ_u^2 in various ways: a) by reducing input coefficient of variability, even to zero by employing metronomic firing patterns. Of course, this can lead to severe temporal output variations due to the periodicity of the input, which may be considered as 'variance' in itself; b) by superimposing many RN input streams. This avoids output periodicity but requires parallelism with low firing rates and hence reduced bandwidth (for transfer of mean rate); c) a combination of the above. The key point is that reduction of σ_u^2 will ultimately unmask PN, σ_p^2, as the dominant component of output variance.

We have not examined the dynamic case. However, if we assume that the uncertainty in the transfer function can be modelled as an extended white noise process with a strength proportional to the mean transfer function, then equation 4 reduces to

$$V\{y(t)\} \approx \int_0^t \left(\bar{p}^2(t-v)(q\bar{u}^2(v) + k|\bar{u}(v)|)\right)dv$$

This is algebraically equivalent to signal dependent noise, in which the variance of the input *r* is proportional to the square of the mean of *r*. The trajectories of point-to-point movements that minimise this variance (without the RN component) have been shown to describe saccadic eye and arm reaching movements remarkably well (Harris & Wolpert, 1998) However, the optimal trajectory that minimises the full model of equation 4 remains to be explored.

4. Conclusion

Uncertainty in time estimation will lead to PN on an analog output, which could explain a wide variety of behavioural phenomena. It seems *a priori* that such uncertainty is inevitable. RN can be reduced by parallelism or by reducing the coefficient of variability of ISI's (although both have limitations). Eventually, PN must emerge. The empirical question is not whether PN exists, but how much of it is there relative to RN.

References

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