

# Maximally reliable Markov chains under energy constraints

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Signal to noise ratios in physical systems can be significantly degraded if the latency or processing time of the system is highly variable. Molecular computations where precise temporal procession is a necessary feature (e.g. the ion channel dynamics involved in action potential generation and membrane refraction) appear to have reduced their processing time variabilities by employing multiple steps. Numerical studies of the activation time of rhodopsin molecules, for example, have revealed that the low variability observed experimentally can only be accounted for by assuming that the molecules shut off by means of a multi-step process, and that, if implemented by the retina, a single-step system would lead to much poorer vision [1]. We generalize this theoretical result and prove that the reliability of the passage time from the first state to the last state in a multi-state system with no memory (i.e. a Markov chain) is maximal if and only if the system proceeds irreversibly through each state from first to last with identical transition rates between all consecutive pairs of states. Specifically, we show that for such a linear Markov chain, the following relation holds:  $\text{var}(t) = \frac{T^2}{N-1}$ , where  $t$  is the passage time through the system,  $T$  is the mean passage time (which we consider to be fixed), and  $N$  is the number of states. The variance of the passage time exceeds this value for any other network topology. It is thus clear that by increasing the number of states, it is possible to arbitrarily decrease the variance of the passage time or, equivalently, increase the reliability of the system.

In a physical system, however, irreversible transitions are implemented by maintaining large energy drops between states. As the number of states in a linear Markov chain increases, the total energy across the length of the chain also increases, and thus infinitely long chains (which would be perfectly reliable) would require infinite energies. To study the effect of energy constraints on Markov chain reliability, we numerically optimized the transition rates between all pairs of states in an  $N$ -state Markov chain to minimize the variance of the passage time while holding  $T$  and the total energy  $E_{tot}$  constant, where transition rates of zero and infinity correspond to energies of infinity and zero respectively. Thus transition rates near zero (needed to prevent reverse transitions in a linear chain) are only possible if  $E_{tot}$  is permitted to be large. We found that as  $E_{tot}$  is decreased, the variance increases as expected, but also that at certain points the linear structure becomes unstable and that states merge to meet the more stringent energy constraint, decreasing the effective number of states. Eventually, at low available energy values, all intermediate states merge with the first, and the system becomes a one-step (i.e. minimally reliable) process. These results suggest that there is a fundamental tradeoff in physical systems between reliability (preferring large, linear Markov chains) and conservation of energy resources (preferring small, fully-connected chains).

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## References

[1] On the reproducibility of single photon responses (SPRs): the gordian knot of rod phototransduction perseveres. R. Hamer, S. Nicholas, D. Tranchina, and P. Liebman, *J. Vis.* 2(10):113-113, Dec. 2002.