# Dynamic sensory information transmission as a function of population size, sensory temporal correlation and single neuron signal-to-noise

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# Questions of interest

–Efficient coding hypothesis discussed by Attneave, Barlow, Atick, et al.

– Performance of population codes as a function of

1. spatial stimulus correlations
2. **temporal stimulus correlations**
3. network noise correlations

**Challenges -** Non-linearity and non-Gaussianity of neural responses

**-** Stimulus distributions with temporal dynamics and correlation structures

# Neural System as a Stochastic Dynamical Process

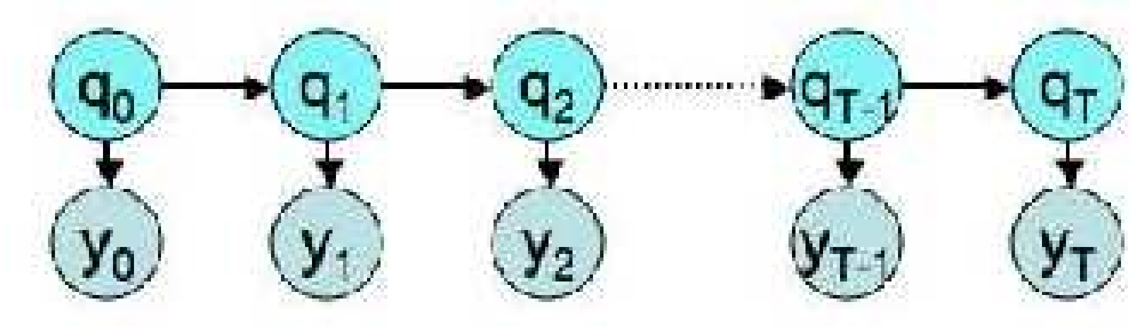


Figure 1: The dynamics of sensory input may be described as a stochastic dynamical process: a state variable $q_t$ evolves through time according to some Markovian dynamics $p(q_t|q_{t-1}, \theta)$, as specified by a few model parameters $\theta$. Neural acitivity $y_t$ are a noisy, subsampled version of $q_t$, summarized by an observation distribution $p(y_t|q_t)$.

- Hidden unobvserved state: $Q := Q_1, Q_2, \cdots, Q_T$

-Noisy observation: $Y := Y_1, Y_2, \cdots, Y_T$

$P(Q, Y) = p(q_1) \prod_{t=2}^{T} p(q_t|q_{t-1}) \prod_{t=1}^{T} p(y_t|q_t)$

# Examples of Stochastic Dynamics

– Hidden unobserved states and Noisy observations:

1. Spatial location of a rate moving in a close environment and the neural activity of place cells.
2. Spatio-temporally varying visual stimuli and the corresponding neural activity in V1.
3. Two-dimensional position of the hand and the activity of multiple simultaneously recorded neurons from the contralateral primary motor cortex.

# Background on High SNR results

– Static sensory input $Q$ and observations from a population of neurons : $R_k\ k = 1, \cdots, n \sim \prod_{k=1}^{n} f(R_k|Q)$
[Clarke and Barron, 1990, Brunel and Nadal, 1998]

$$I(\{R_1, \cdots, R_n\}; Q) = H(Q) - \mathrm{E}_Q \left[ \log \sqrt{\frac{2\pi e}{nJ(Q)}} \right]$$

– time varying stationary sensory input $Q_t$ and observations from a population of neurons : $\{R_1(t), \cdots, R_n(t)\} \sim \prod_{k=1}^{n} f(R_k(t)|Q_t)$

$$I(\{R_1(t), \cdots, R_n(t)\}_{1:T}; Q_{1:T}) = H(Q_{1:T}) - T\mathrm{E}_Q \left[ \log \sqrt{\frac{2\pi e}{nJ(Q)}} \right]$$

$$\begin{aligned} I(\{R_1(t), \cdots, R_n(t)\}_{1:T}; Q_{1:T}) - \sum_{t=1}^{T} I(R_t; Q_t) &= H(Q_{1:T}) - \sum_{t=1}^{T} H(Q_t) \\ &= T\left[H(Q_1|Q_0) - H(Q_1)\right] \end{aligned}$$

where $J(q) := -E_R \partial_q^2 \log f(R|q)]$.

# Background on Low SNR results: Dynamic Stimuli

– Observations available from a few weakly tuned neurons. LNP model : $R|Q \sim \text{Poiss}(\lambda(\epsilon Q))$

$$Q_T^{\text{MAP}} \approx \epsilon \sigma_Q^2 \sum_{t=1}^{T} \left( \frac{\lambda'}{\lambda} R_t - \lambda' \right) e^{-(T-t)dt/\tau}$$

– Maximum a posteriori (MAP) estimate is Linear in the responses [Bialek and Zee, 1990, Pillow et al., 2009] for a finite number of neurons.

$g_1(R) = \frac{\lambda'}{\lambda}(0) R - \lambda'(0)$

# Information rates of temporally correlated stimuli: Low SNR regime

$$
\begin{aligned}
I(R_{1:T}; Q_{1:T}) &\approx \sum_{t=1}^{T} I(R_t; Q_t) \approx T\frac{\epsilon^2 J}{2}\sigma_Q^2 \\
I(R_{1:T}; Q_T) &\approx \frac{\epsilon^2 J}{2} \sum_{t=1}^{T} \mathrm{var}_{Q_T}\left[\mathrm{E}(Q_t | Q_T)\right] \\
&= \frac{\epsilon^2 \sigma_Q^2 J}{2} \sum_{t=1}^{T} \mathrm{cor}\left[Q_t, Q_T\right] \qquad \text{for Gaussian} \quad Q_t
\end{aligned}
$$

1. Time varying stationary sensory input $\mathrm{E}[Q_0 Q_t] \sim e^{-t/\tau}$
2. Neurons are only weakly tuned to the stimulus properties, or equivalently that the stimulus magnitude is relatively small. $R_t \sim f(y_t | \epsilon q_t)$ for $\epsilon << 1$.
3. Define Fisher information $J := -E_R[\partial_q^2 \log f(R|q)]|_{q=0}$.

# LNP neuron with temporally correlated sensory input

$$I(Q_T; R_{1:T}) \approx \frac{\epsilon^2 \sigma_Q^2 J}{2} \sum_{t=1}^{T} \mathrm{cor}\left[Q_t, Q_T\right] = \frac{\epsilon^2 \sigma_Q^2 J}{2} \sum_{t=1}^{T} e^{-(T-t)dt/\tau}$$

$$= \frac{\epsilon^2 \sigma_Q^2 J}{2} \frac{1 - e^{-T dt/\tau}}{1 - e^{-dt/\tau}}$$

1. dynamics : $dq_t = -\tau^{-1} q_t + \sigma dB_t$ or, $q_{t+dt} = e^{-dt/\tau} q_t + \sigma \sqrt{dt} \epsilon_t$
2. $\mathrm{cov}(q_0, q_{kdt}) = \frac{\tau \sigma^2}{2} e^{-kdt/\tau}$ and $\sigma_Q^2 = \frac{\tau \sigma^2}{2}$
3. neural responses: $R_i(t) \sim \mathrm{Poiss}(f_i(\epsilon q_t) dt)$ for $i = 1, \cdots, n$

– mutual information increases linearly with the number of neurons

$$J := \sum_{i=1}^{n} \left[ -f_i \left(\frac{f_i'}{f_i}\right)' + f_i'' \right]_{q=0} dt$$

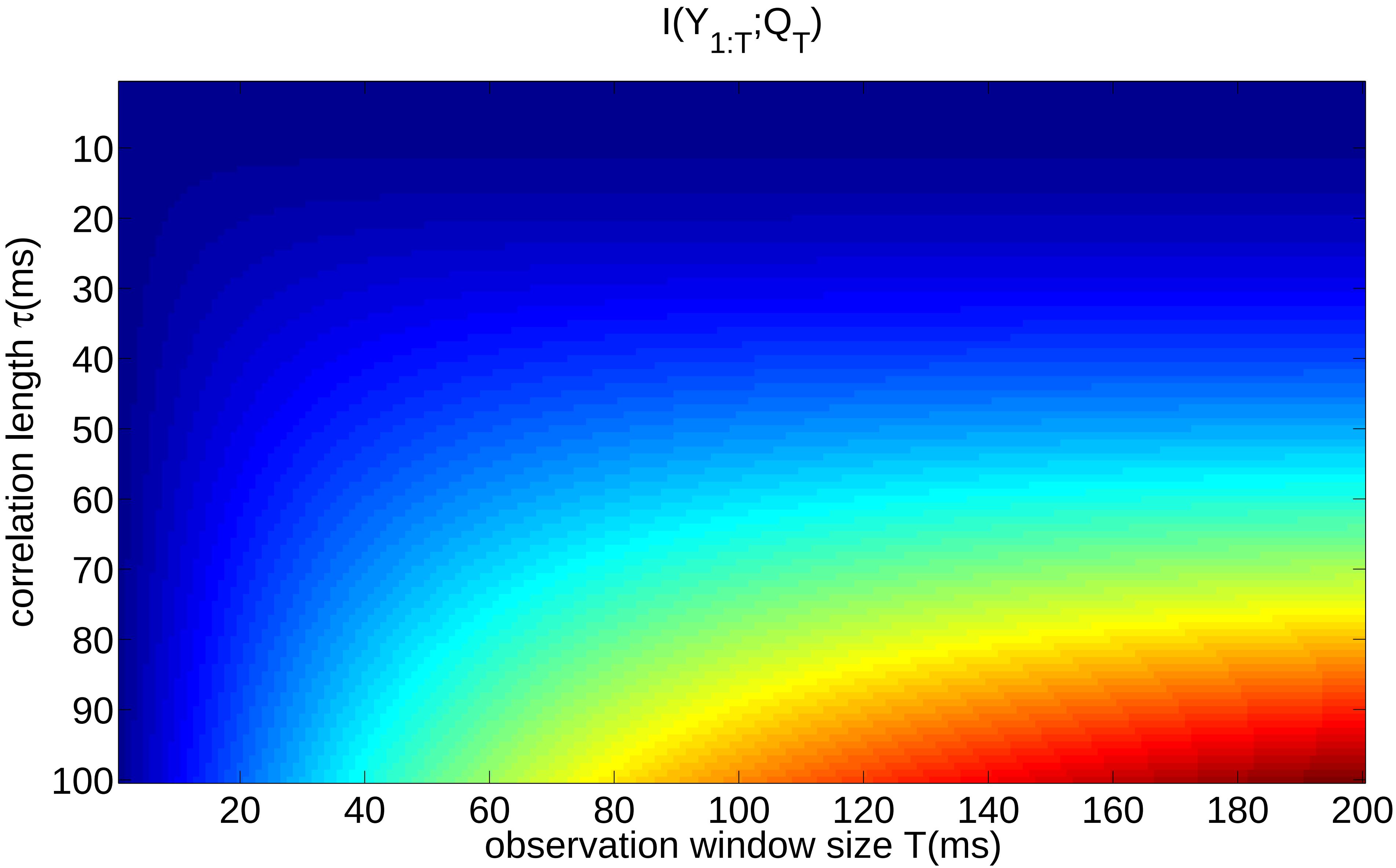


Figure 2: Colormap of $I(Q_T; R_{1:T})$ as a function of $\tau$ and $T$.

# Information rates of temporally correlated stimuli: Intermediate SNR regime

1. Observations available from a large population of neurons, i.e. $n \to \infty$
2. Neurons are only weakly tuned to the stimulus properties, or equivalently that the stimulus magnitude is relatively small. $R_k(t) \sim f(r_k(t)|\epsilon q_t)$ for $\epsilon \sim n^{-1/2}$.
3. We have $n$ neurons with SNR$\sim n^{-1}$.

# Information rates of temporally correlated stimuli: Intermediate SNR regime

– Observations from
$\{R_1(t), \cdots, R_n(t)\} \sim \prod_{k=1}^{n} f(R_k(t)|\frac{Q_t}{\sqrt{n}})$
is equivalent to the
*Linear Gaussian Additive* model:
$Z_t = Q_t + e_t$ where $e_t \sim \mathcal{N}(0, J_0^{-1})$

– $Z_t = \frac{1}{\sqrt{nJ_0}} \sum_{k=1}^{n} \left( \frac{\partial \log f(R_k(t)|q)}{\partial q} \right)_{q=0}$
is approximately(assymptotically) sufficient statistics

# Large Population of LNP neurons receiving temporally correlated stimuli

$$Z_t = \sum_{k=1}^{n} \left( \frac{R_k(t)}{\lambda_0 dt \sqrt{n}} - \frac{1}{\sqrt{n}} \right) = Q_t + e_t \qquad \mathrm{var}[e_t] = (\lambda_0 dt)^{-1}$$

1. dynamics : $Q_{t+dt} = e^{-dt/\tau} Q_t + \sigma \sqrt{dt} \epsilon_t$
2. neural responses: $R_i(t) \sim \mathrm{Poiss}(\lambda_0 e^{q_t/\sqrt{n}} dt)$ for $i = 1, \cdots, n$

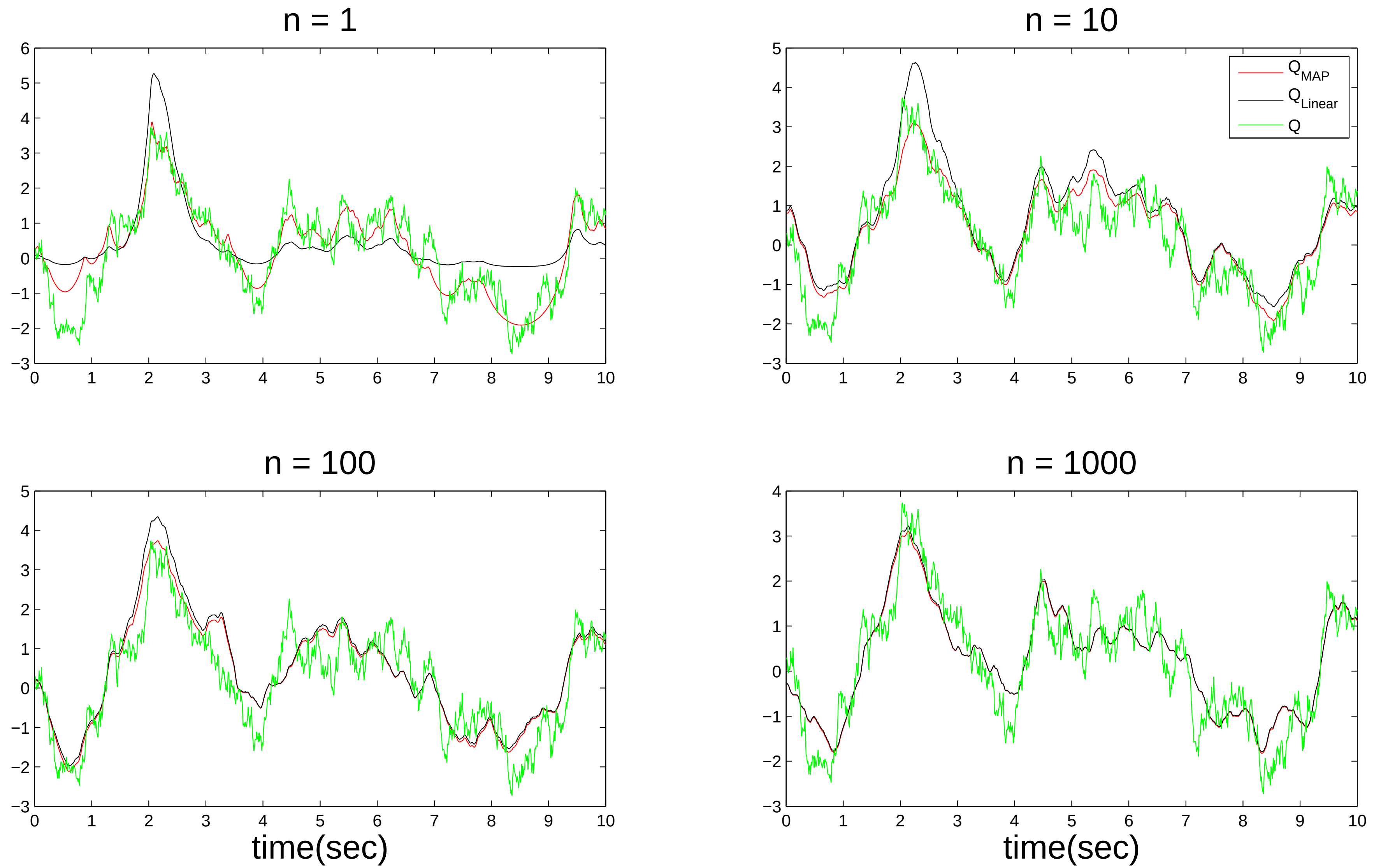


Figure 3: MAP estimate(red) of $Q_t$ (green) based on full spiking activity compared to a simple linear estimate(black) based on linear transformation of the sum of spikes $\sum_{k=1}^{n} R_k(t)$.

# Summary

1. The information rate can be characterized by the *temporal correlation* $\tau$ of the stimuli, *population size* $n$, and *single neuron SNR* $\epsilon$.

2. The effective population size is $\sim n\epsilon\tau^{1/2}$ and the total power of the population is $\sim n\epsilon^2$.

3. In the intermediate SNR regime, regardless of the population size, the total energy of the neural activity is fixed. Therefore, the right scaling is $\epsilon \sim 1/\sqrt{n}$. In this regime, a *linear* decoder achieves the optimal performance of a non-linear MAP decoder.

– Main assumption is that given the stimuli, the neural activity of the population is *independent*. A natural next step is to include the spike history effects.

# Appendix: calculations

$$
\begin{aligned}
p(y_t|q_t) &= f_0(y_t)\left[1+\epsilon g_1(y_t)q_t+\frac{\epsilon^2}{2}g_2(y_t)q_t^2+O(\epsilon^3)\right] \\
P(Y_{1:T}|Q_T) &= \mathrm{E}_{Q_{1:T-1}}\left[\prod_{t=1}^{T}p(Y_t|Q_t)|Q_T\right] \\
&= \prod_{t=1}^{T}f_0(y_t)\left[1+\epsilon\sum_{t=1}^{T}g_1(y_t)\mathrm{E}[Q_t|Q_T]+\frac{\epsilon^2}{2}\sum_{t=1}^{T}g_2(y_t)\mathrm{E}[Q_t^2|Q_T]+\epsilon^2\sum_{t\neq t'}g_1(y_t)g_1(y_{t'})\mathrm{E}[Q_tQ_{t'}|Q_T]\right] \\
P(Y_{1:T}) &= \mathrm{E}_{Q_{1:T}}\left[\prod_{t=1}^{T}p(Y_t|Q_t)\right] \\
&= \prod_{t=1}^{T}f_0(y_t)\left[1+\epsilon\sum_{t=1}^{T}g_1(y_t)\mathrm{E}[Q_t]+\frac{\epsilon^2}{2}\sum_{t=1}^{T}g_2(y_t)\mathrm{E}[Q_t^2]+\epsilon^2\sum_{t\neq t'}g_1(y_t)g_1(y_{t'})\mathrm{E}[Q_tQ_{t'}]\right] \\
&= \mathrm{E}_{Q_{1:T}}\left[\prod_{t=1}^{T}p(Y_t|Q_t)\right] \\
&= \prod_{t=1}^{T}f_0(y_t)\left[1+\frac{\epsilon^2}{2}\sum_{t=1}^{T}g_2(y_t)\mathrm{E}[Q_t^2]+\epsilon^2\sum_{t\neq t'}g_1(y_t)g_1(y_{t'})\mathrm{E}[Q_tQ_{t'}]\right] \\
Q_T^{\mathrm{MAP}} &= -\frac{\epsilon}{\partial_2\log p(Q_T)|_{Q_T=0}}\sum_{t=1}^{T}g_1(y_t)\partial\left(\mathrm{E}\left[Q_t|Q_T\right]\right)|_{Q_T=0}+O(\epsilon^2)
\end{aligned}
$$

# Appendix: calculations

$$\begin{aligned} q_{t+1} &= Aq_t + e_t \qquad \mathrm{cov}[e_t] = C_q \\ y_t &= Bq_t + n_t \quad \mathrm{cov}[n_t] = C_y \end{aligned}$$

$$\begin{aligned} C^f &= \left[(AC^f A^T + C_q)^{-1} + B^T C_y^{-1} B\right]^{-1} \\ C^s &= C^f + J\left[C^s - AC^f A^T - C_q\right] J^T, \\ J &:= C^f A^T \left[AC^f A^T + C_q\right]^{-1} \\ C^s - JC^s J^T &= C^f - J\left[AC^f A^T + C_q\right] J^T = C^f - C^f A^T \left[AC^f A^T + C_q\right]^{-1} AC^f \end{aligned}$$

# Appendix: calculations

When $q$ is one-dimensional, define:

$$x := C^f \quad \text{and} \quad a := A \quad \beta := B^T C_y^{-1} B \quad \sigma^2 = C_q,$$

then,

$$\begin{aligned} x &= \left[(a^2 x + \sigma^2)^{-1} + \beta\right]^{-1} \\ x &= \frac{-(\beta\sigma^2 - a^2 + 1) + \sqrt{(\beta\sigma^2 - a^2 + 1)^2 + 4a^2\beta\sigma^2}}{2\beta a^2} \\ J &= \frac{xa}{a^2 x + \sigma^2} \\ C^s - JC^s J^T &= x - \frac{a^2 x^2}{a^2 x + \sigma^2} = \frac{x\sigma^2}{a^2 x + \sigma^2} \end{aligned}$$

$$\begin{aligned} \lim_{T\to\infty} \frac{1}{T} I(Q_{1:T}; Y_{1:T}) &= \frac{1}{2}\log \frac{|C_q|}{|C^s - JC^s J^T|} = \frac{1}{2}\log \frac{\sigma^2}{\left(\frac{\sigma^2}{a^2+\sigma^2/x}\right)} = \frac{1}{2}\log\left(a^2 + \sigma^2/x\right) \\ I(Q_T; Y_T) &= \frac{1}{2}\log \frac{|C_y + BB^T\sigma^2/(1-a^2)|}{|C_y|} = \frac{1}{2}\log\left(1 + \frac{\sigma^2\beta}{1-a^2}\right) \end{aligned}$$

# References


[Bialek and Zee, 1990] Bialek, W. and Zee, A. (1990). Coding and computation with neural spike trains. *Journal of Statistical Physics*, 59:103–115.

[Brunel and Nadal, 1998] Brunel, N. and Nadal, J.-P. (1998). Mutual information, fisher information, and population coding. *Neural Comput.*, 10(7):1731–1757.

[Clarke and Barron, 1990] Clarke, B. and Barron, A. (1990). Information-theoretic asymptotics of Bayes