

Optimal population coding

1 Fisher information bound

Consider a population of N neurons encoding a one-dimensional stimulus s via their vector of spike counts \mathbf{c} . The mutual information between the spike counts \mathbf{C} and the stimulus s assumed fixed over a typical time τ is bounded below by the Fisher information bound $I_F(\mathbf{C}, s)$

$$I(\mathbf{c}, s) \geq I_F(\mathbf{c}, s) = H(s) + \frac{1}{2} \int_{s_-}^{s_+} ds p(s) \log_2 \left(\frac{F_{\mathbf{c}}(s)}{2\pi e} \right), \quad (1)$$

where $F_{\mathbf{c}}(s)$ is the Fisher information associated with the statistical model $p(\mathbf{c}|s)$. For a population of independent Poissonian neurons with tuning curves $f_i(s)$, the Fisher information is simply:

$$F_{\mathbf{c}}(s) = F_{\mathbf{f}}^N(s)\tau \quad \text{where} \quad F_{\mathbf{f}}^N(s) = \sum_i^N \frac{f'_i(s)^2}{f_i(s)} \quad (2)$$

Unless otherwise specified, we drop the dependence over the typical integration time τ , i.e. we assume $\tau = 1$. To investigate encoding schemes that favor information transfer, we search of tuning curves combinations that optimize the Fisher information bound $I_F(s, \mathbf{c})$. In other words, we consider the problem of optimizing

$$\mathcal{F}(\mathbf{f}) = \int_{s_-}^{s_+} ds p(s) \log_2 \left(\sum_i^N \frac{f'_i(s)^2}{f_i(s)} \right) \quad (3)$$

by varying the tuning curves $f_i(s)$ while holding the stimulus distribution $p(s)$ fixed. To be well-posed, this problem requires additional constraints such as imposing a finite range of variation to the tuning curve or a fixed mean firing rate to the overall population. In any case, the problem is a non-convex optimization problem.

Suppose we pool neurons that have identical tuning curves in K populations, each comprising n_i neurons, $1 \leq n_i \leq K$. Then the Fisher information reads

$$F_{\mathbf{f}}^{K,\mathbf{n}}(s) = \sum_i^K n_i \frac{f'_i(s)^2}{f_i(s)} \quad \text{with} \quad \sum_i^P n_i = N. \quad (4)$$

Interestingly, reading independently the output of distinct neurons from the same population does not yield any information benefit over reading out their overall population activity jointly. Indeed the population readout is a Poisson process with rate $n_i f_i(s)$, which yields the same contribution to the Fisher information $F_C(s)$ since we have:

$$\frac{(n_i f'_i(s))^2}{n_i f_i(s)} = \frac{n_i f'_i(s)^2}{f_i(s)}. \quad (5)$$

Thus, neurons that share the same tuning curve are equally informative when considered together or independently.

However, constraining distinct neurons to have the same tuning curve ($n_i > 1$ for some i or $K < N$) shall incur an information cost as it limits the optimization of the functional $F_{\mathbf{f}}^{K,\mathbf{n}}(s)$ to a more restricted space of tuning curves. Stated equivalently, there shall be an information gain to split an homogeneous population of neurons with identical tuning curves into subpopulations of neurons with distinct tuning curves.

1.1 Constrained optimization problem for one population

Consider a redundant population of N neurons with identical tuning curves. Optimizing the corresponding Fisher bound amounts to maximizing

$$\mathcal{F}^{(1)}(f) = \int_{s_-}^{s_+} ds p(s) \log_2 \left(\frac{N f'(s)^2}{f(s)} \right) \quad (6)$$

with respect to the tuning curve $f(s)$, which is a problem in the calculus of variations. Introducing the Lagrangian integrand $\mathcal{L}(f, f', s) = p(s) \log_2 (f'(s)^2 / f(s))$, the stationary curves of $\mathcal{F}^{(1)}$ satisfy the Euler-Lagrange equation:

$$\frac{\partial \mathcal{L}}{\partial f} - \frac{d}{ds} \left[\frac{\partial \mathcal{L}}{\partial f'} \right] = \frac{p(s)}{f(s)} + 2 \frac{d}{ds} \left[\frac{p(s)}{f'(s)} \right] = 0 \quad (7)$$

Upon multiplication by $f'(s)/p(s)$, we have

$$\frac{f'(s)}{f(s)} + 2 \frac{d}{ds} \left[\frac{p(s)}{f'(s)} \right] \frac{f'(s)}{p(s)} = \frac{d}{ds} \left[\ln \left(\frac{f(s)p(s)^2}{f'(s)^2} \right) \right] = 0, \quad (8)$$

so that stationary tuning curves satisfy the first-order equation

$$\frac{f'(s)^2}{f(s)} = Qp(s)^2, \quad (9)$$

where Q is a constant to be determined via the constraints of the optimization problems. Specifically, considering increasing tuning curves ($f'(s) > 0$) satisfying boundary conditions $f(s_-) = f_-$ and $f(s_+) = f_+$, we must have

$$\sqrt{Q} = \sqrt{Q} \int_{s_-}^{s_+} p(s) ds = \int_{s_-}^{s_+} \frac{f'(s)}{\sqrt{f(s)}} ds = 2 \left(\sqrt{f_+} - \sqrt{f_-} \right), \quad (10)$$

which specifies the stationary tuning curves as

$$f^*(s) = \left(\sqrt{f_-} + (\sqrt{f_+} - \sqrt{f_-})P(s) \right)^2, \quad (11)$$

where $P(s)$ is the cumulative distribution of the stimulus $P(s) = \int_{s_-}^s p(s) ds$. Using the above expression for stationary curves, we can evaluate the stationary Fisher information bound in equation (1):

$$I_F^{(1)}(f^*) = H(s) + \frac{1}{2} \int_{s_-}^{s_+} ds p(s) \log_2 \left(\frac{2N (\sqrt{f_+} - \sqrt{f_-})^2 p(s)^2}{\pi e} \right) \quad (12)$$

$$= \log_2 \left(\sqrt{2N} \left(\sqrt{f_+} - \sqrt{f_-} \right) / \sqrt{\pi e} \right). \quad (13)$$

The second order variations of $I_F^{(1)}$ defines a negative quadratic form showing that $I_F^{(1)}$ achieves a local maximum at the stationary path. Because there is a unique stationary path compatible with the boundary conditions of the problem, this local maximum is the global maximum.

It turns out that, with the additional assumption that tuning curves are increasing, the variational problem can be transformed into a simpler constrained optimization problem. Indeed, operating the change of variable $f'/\sqrt{f} = h$ leads to the problem of optimizing

$$\mathcal{H}^{(1)}(h) = \int_{s_-}^{s_+} ds p(s) \log_2 (Nh(s)^2), \quad (14)$$

over the constrained set \mathcal{C} of functions $h(s)$ satisfying

$$\int_{s_-}^{s_+} h(s) ds = 2 \left(\sqrt{f_+} - \sqrt{f_-} \right) \quad \text{and} \quad h(s) \geq 0. \quad (15)$$

Although this optimization problem is not convex, it is well-posed. Moreover, if one finds the function $h^*(s)$ that optimizes $\mathcal{H}^{(1)}(h)$, one can recover the corresponding tuning curve $f^*(s)$ by integrating $f'(s)/\sqrt{f(s)} = h^*(s)$ with boundary conditions $f(s_-) = f_-$ and $f(s_+) = f_+$. To solve the constrained optimization problem, we introduced the Lagrangian function

$$\begin{aligned} \mathcal{H}^{(1)}(h, \lambda, \mu) = & \int_{s_-}^{s_+} ds p(s) \log_2 (N h(s)^2) \\ & + \lambda \left(\int_{s_-}^{s_+} h(s) ds - 2 \left(\sqrt{f_+} - \sqrt{f_-} \right) \right) + \int_{s_-}^{s_+} \mu(s) h(s) ds \end{aligned} \quad (16)$$

where λ and $\mu(s)$ are Lagrange multipliers associated with both constraints. Notice that the Lagrangian $\mathcal{H}^{(1)}(h, \lambda, \mu)$ is defined as a function of λ and $\mu(s)$ such that

$$\sup_{h \in \mathcal{C}} \mathcal{H}^{(1)}(h) = \sup_h \inf_{\lambda, \mu \geq 0} \mathcal{H}^{(1)}(h, \lambda, \mu). \quad (18)$$

As the Lagrangian integrand diverges negatively when the function $h(s)$ vanishes, the positive constraints $h(s) \geq 0$ will not to be qualified for curves that optimize $\mathcal{H}^{(1)}(h)$. In fact, we could have omitted the constraints of positivity in the formulation of our one-population optimization problem. However, these constraints play an important role for the case of multiple populations with distinct tuning curves. In the case of a single population, the stationary curves $h^*(s)$ must be interior points, i.e. $h(s) > 0$, which necessarily satisfy the Karush-Kuhn-Tucker conditions:

$$\frac{\delta \mathcal{H}^{(1)}(h)}{\delta h(s)} = \frac{2p(s)}{h^*(s)} + \lambda + \mu(s) = 0, \quad \text{with} \quad \mu(s) \leq 0. \quad (19)$$

The complementary slackness condition $\mu(s)h(s) = 0$ implies that $\mu(s) = 0$ and that $h(s) = -\lambda p(s)/2$ with

$$\lambda = \lambda \int_{s_-}^{s_+} p(s) ds = -2 \int_{s_-}^{s_+} h^*(s) ds = -4 \left(\sqrt{f_+} - \sqrt{f_-} \right). \quad (20)$$

The above relation implies that $h^*(s) = 2 \left(\sqrt{f_+} - \sqrt{f_-} \right) p(s)$. One can check that solving for f^* given h^* yields the same increasing tuning curve as the one obtained by calculus in the variations.

1.2 Constrained optimization problem for multiple populations

Keeping our assumption that tuning curves are increasing, we optimize for the Fisher information bound $I_F^{(2)}$ for two populations of n_1 cells and n_2 cells, each

with their tuning curves $f_1(s)$ and $f_2(s)$. To solve this problem, we consider the Lagrangian function

$$\mathcal{H}^{(2)}(h_1, h_2) = \int_{s_-}^{s_+} ds p(s) \log_2 (n_1 h_1(s)^2 + n_2 h_2(s)^2) \quad (21)$$

$$+ \lambda_1 \left(\int_{s_-}^{s_+} h_1(s) ds - \sqrt{2}(f_+ - f_-) \right) \quad (22)$$

$$+ \lambda_2 \left(\int_{s_-}^{s_+} h_2(s) ds - \sqrt{2}(f_+ - f_-) \right) \quad (23)$$

$$+ \int_{s_-}^{s_+} \mu_1(s) h_1(s) ds + \int_{s_-}^{s_+} \mu_2(s) h_2(s) ds, \quad (24)$$

where λ_1 , $\mu_1(s)$ and λ_2 , $\mu_2(s)$ are Lagrange multipliers associated with the constraints on the auxiliary functions $h_1(s) = f'_1(s)/\sqrt{f_1(s)}$ and $h_2(s) = f'_2(s)/\sqrt{f_2(s)}$, respectively. Importantly, in the two-dimensional optimization setting, the stationary curves $(h_1^*(s), h_2^*(s))$ are not necessarily interior points. Indeed, one function (e.g. $h_1^*(s)$) can be zero without incurring a negative divergence of the Lagrangian integrand if the other function (e.g. $h_2^*(s)$) is nonzero. In any case, the Karush-Kuhn-Tucker criterion still gives necessary conditions for stationary curves:

$$\frac{\delta \mathcal{H}^{(2)}(\mathbf{h})}{\delta h_1(s)} = \frac{2p(s)n_1 h_1(s)}{n_1 h_1(s)^2 + n_2 h_2(s)^2} + \lambda_1 + \mu_1(s) = 0, \quad (25)$$

$$\frac{\delta \mathcal{H}^{(2)}(\mathbf{h})}{\delta h_2(s)} = \frac{2p(s)n_2 h_2(s)}{n_1 h_1(s)^2 + n_2 h_2(s)^2} + \lambda_2 + \mu_2(s) = 0. \quad (26)$$

Moreover, and perhaps more informatively, the second variation of the Lagrangian $\mathcal{H}^{(2)}(h_1, h_2)$ involves a quadratic form defined by the Hessians

$$\frac{\delta^2 \mathcal{H}^{(2)}(\mathbf{h})}{\delta h_1^2(s)} = -\frac{\delta^2 \mathcal{H}^{(2)}(\mathbf{h})}{\delta h_2^2(s)} = \frac{2p(s)(n_2 h_2(s)^2 - n_1 h_1(s)^2)}{(n_1 h_1(s)^2 + n_2 h_2(s)^2)^2} \quad (27)$$

$$\frac{\delta^2 \mathcal{H}^{(2)}(\mathbf{h})}{\delta h_1(s) \delta h_2(s)} = -\frac{4p(s)n_1 n_2 h_1(s) h_2(s)}{(n_1 h_1(s)^2 + n_2 h_2(s)^2)^2} = 0 \quad (28)$$

which all have a negative and a positive eigenvalues. As a consequence, no stationary curves $(h_1^*(s), h_2^*(s))$ can be an interior point, i.e. such that $h_1(s) > 0$ and $h_2(s) > 0$, on some non-zero measure set. In other words, stationary curves $(h_1^*(s), h_2^*(s))$ are sensitive to the stimulus s on mutually exclusive supports. Although not mathematically necessary, the biologically relevant choice of supports is to consider two contiguous intervals separated by s_0 : (s_-, s_0) and (s_0, s_+) .

One each of these intervals, only one population is sensitive to the stimulus, e.g. $h_1 > 0, h_2 = 0$ on (s_-, s_0) and $h_1 = 0, h_2 > 0$ on (s_0, s_+) . When considered on (s_-, s_0) and (s_0, s_+) , the two-dimensional optimization problem becomes a one-dimensional problem and we have

$$h_1^*(s) = 2(\sqrt{f_+} - \sqrt{f_-}) \left(\frac{p(s)}{P_0} \right), \quad (29)$$

$$h_2^*(s) = 2(\sqrt{f_+} - \sqrt{f_-}) \left(\frac{p(s)}{1 - P_0} \right), \quad (30)$$

where we have defined $P_0 = P(s_0)$. Using the above expressions for stationary curves, we can evaluate the stationary Fisher information bound:

$$I_F^{(2)}(f_1^*, f_2^*) = H(s) \quad (31)$$

$$+ \frac{1}{2} \int_{s_-}^{s_0} ds p(s) \log_2 \left(\frac{2n_1}{\pi e} \left((\sqrt{f_+} - \sqrt{f_-}) \frac{p(s)}{P_0} \right)^2 \right) \quad (32)$$

$$+ \frac{1}{2} \int_{s_0}^{s_+} ds p(s) \log_2 \left(\frac{2n_2}{\pi e} \left((\sqrt{f_+} - \sqrt{f_-}) \frac{p(s)}{1 - P_0} \right)^2 \right) \quad (33)$$

$$= \log_2 \left(\sqrt{2} (\sqrt{f_+} - \sqrt{f_-}) / \sqrt{\pi e} \right) \quad (34)$$

$$+ P_0 \log_2 \left(\frac{\sqrt{n_1}}{P_0} \right) + (1 - P_0) \log_2 \left(\frac{\sqrt{n_2}}{1 - P_0} \right). \quad (35)$$

In turn, optimizing with respect to the probability mass P_0 yields

$$I_F^{(2)}(f_1^*, f_2^*) = \log_2 \left(\sqrt{2} (\sqrt{f_+} - \sqrt{f_-}) / \sqrt{\pi e} \right) + \log_2 (\sqrt{n_1} + \sqrt{n_2}), \quad (36)$$

which is attained for allotting probability mass in proportion to the square root of the population sizes:

$$P_0 = \frac{\sqrt{n_1}}{\sqrt{n_1} + \sqrt{n_2}}. \quad (37)$$

After a last optimization over the population size n_1, n_2 , with $n_1 + n_2 = N$, we obtain

$$I_F^{(2)}(f_1^*, f_2^*) = \log_2 \left((\sqrt{f_+} - \sqrt{f_-}) / \sqrt{\pi e} \right) + \log_2 (2\sqrt{N}), \quad (38)$$

which is $\log_2 \sqrt{2} = 1/2$ bits more than $I_F^{(1)}(f^*)$. We can generalize this result for K populations of n_i neurons with $\sum n_i = N$, each with their own increasing tuning curves $f_i(s)$. The optimal Fisher information bound is $I_F^{(K)}(\mathbf{f}^*)$ is attained for

equally distributed populations of $n_i = N/K$ cells, with tuning curves $f_i(s)$ that are sensitive to mutually exclusive ranges of stimulus. Specifically, these ranges $(s_{i,-}, s_{i,+})$ form a partition of the stimulus space with equal probability mass, i.e. $P(s_{i,+}) - P(s_{i,-}) = 1/K$ and we have

$$f_i^*(s) = \left(\sqrt{f_-} + (\sqrt{f_+} - \sqrt{f_-})K(P(s) - P(s_{i,-})) \right)^2, \quad (39)$$

For such populations of tuned curves, the optimal Fisher bound is

$$I_F^{(K)} = \log_2 \left(\left(\sqrt{f_+} - \sqrt{f_-} \right) / \sqrt{\pi e} \right) + \log_2 \left(\sqrt{2KN} \right), \quad (40)$$

showing that the information gain warranted by splitting the population in K independent populations can be as high as $(\log_2 K)/2$ bits. Thus, in principle, information transfer can be improved by half a bit each time the number of tuning curves is doubled.

1.3 Monotonicity and average rate constraints

Up to this point, all our results are obtained under the constraint of finite range of variation for the individual neuronal firing rate, with the additional constraint of having monotonic tuning curves. how would these results change once either of these constraints are relaxed?

Given the probability of stimulus presentation $p(s)$, the average firing rate of a neuron with optimal tuning curve $f_i^*(s)$ over its range of sensitivity S_i can be integrated via change of variables

$$\int_{s_{i,-}}^{s_{i,+}} ds p(s) f_i^*(s) = \int_0^{1/K} dP \left(\sqrt{f_-} + (\sqrt{f_+} - \sqrt{f_-})KP \right)^2, \quad (41)$$

$$= \frac{1}{K(\sqrt{f_+} - \sqrt{f_-})} \int_{\sqrt{f_-}}^{\sqrt{f_+}} df f^2. \quad (42)$$

The tuning curve $f_i^*(s)$ encodes no information about the stimulus because it is insensitive to the stimulus outside the support S_i . To be non-informative over a given stimulus range, the tuning curve $f_i(s)$ only has to be constant independent of its constant firing value. At the cost of introducing a discontinuity, but consistent with favoring low firing rate at equal performance, we will assume that neurons fire at their base minimum level when insensitive. With this convention, the overall average firing rate $\bar{f}(K)$ of a neuron among a population of K optimally tuned neurons is

$$\bar{f}(K) = \int_{s_-}^{s_+} ds p(s) f_i^*(s) = f_- \left(1 - \frac{1}{K} \right) + \frac{f_+ + \sqrt{f_+ f_-} + f_-}{3K}. \quad (43)$$

Surprisingly, the average firing rate $\bar{f}(K)$ is a decreasing function of the number of populations as indicated by

$$\bar{f}'(K) = -\frac{1}{3K^2} \left(\sqrt{f_+} + 2\sqrt{f_-} \right) \left(\sqrt{f_+} - \sqrt{f_-} \right) < 0 \quad \text{if } f_+ > f_- . \quad (44)$$

In other word, splitting neural population into tuned subpopulations can increase mutual information between stimulus and neural activity, while lowering the overall average firing neural firing rate. This improvement—warranted ad infinitum based on Fisher information bound calculations—is clearly not realistic for highly divided neural populations, with small, noisy, albeit tuned, sub-populations.

Let us now relax having monotonic tuning curves

$$\bar{g}(K) = \int_{s_-}^{s_+} ds p(s) g_i^*(s) = g_- \left(1 - \frac{2}{K} \right) + \frac{2(g_- + \sqrt{g_+ g_-} + g_-)}{3K} \quad (45)$$

Solving $\bar{g}(K) = \bar{f}(K)$ with $g_- = f_-$ yields $g_+ = G(f_-, f_+)^2 f_+ / 2$ with

$$G(f_-, f_+) = \sqrt{1 + \sqrt{\frac{f_-}{f_+}} + \frac{5}{2} \frac{f_-}{f_+}} - \sqrt{\frac{1}{2} \frac{f_-}{f_+}} > 1 \quad (46)$$

The information gain is independent of K , the number of tuned populations, and is equal to $\log_2 (G(f_-, f_+))$, which vanishes for large dynamic ranges f_+/f_- , but may become beneficial for small dynamic ranges f_+/f_- as

$$\lim_{f_+ \rightarrow f_-} \log_2 (G(f_-, f_+)) = 3/2 \text{ bits} . \quad (47)$$

2 Exact mutual information under population splitting

Without loss of generality, we can assume that the stimulus is uniformly distributed $p(s) = 1/(s_+ - s_-)$ and all results can be recovered by a change of variable over the stimulus space.

2.1 Fundamental bounds under population expansion

FIX KL DIVERGENCE and \log_2 !

$$p(s) = 1/(s_+ - s_-) \quad (48)$$

$$p_-(c) = \frac{(f_-\tau)^c}{c!} e^{-f_-\tau} \quad \text{and} \quad p_+(c) = \frac{(f_+\tau)^c}{c!} e^{-f_+\tau} \quad (49)$$

$$p(\mathbf{c}|s \in S_i) = p_i(\mathbf{c}) = \left(\prod_{j \neq i} p_-(c_j) \right) p_+(c_i) \quad (50)$$

$$p(\mathbf{c}) = \frac{1}{K} \sum_{i=1}^K \left(\prod_{j \neq i} p_-(c_j) \right) p_+(c_i) \quad (51)$$

$$q(\mathbf{c}) = \prod_j p_-(c_j) \quad (52)$$

$$I(\mathbf{c}, s) = H(\mathbf{c}) - \int_{s_-}^{s_+} ds p(s) H(\mathbf{c}|s) \quad (53)$$

$$= - \sum_{\mathbf{c}} p(\mathbf{c}) \log_2(p(\mathbf{c})) + \frac{1}{K} \sum_{i=1}^K p_i(\mathbf{c}) \log_2(p_i(\mathbf{c})) \quad (54)$$

$$= - \sum_{\mathbf{c}} p(\mathbf{c}) \log_2 \left(\frac{p(\mathbf{c})}{q(\mathbf{c})} \right) + \frac{1}{K} \sum_{i=1}^K p_i(\mathbf{c}) \log_2 \left(\frac{p_i(\mathbf{c})}{q(\mathbf{c})} \right) \quad (55)$$

$$= -D_{KL}(p(\mathbf{c})\|q(\mathbf{c})) + D_{KL}(p_i(\mathbf{c})\|q(\mathbf{c})) \quad (56)$$

$$D_{KL}(p_i(\mathbf{c})\|q(\mathbf{c})) = D_{KL}(p_+(c)\|p_-(c)) \quad (57)$$

$$= f_+\tau \left(\log_2 \left(\frac{f_+}{f_-} \right) - 1 \right) + f_-\tau \quad (58)$$

IT IS ALWAYS BETTER TO DETECT f_+ AMONG f_- RATHER THAN f_- AMONG f_+ BECAUSE $D_{KL}(p_+(c)\|p_-(c)) \geq D_{KL}(p_-(c)\|p_+(c))$

$$D_{KL}(p(\mathbf{c})\|q(\mathbf{c})) = \mathbb{E}_q [M_K \log_2(M_K)] \quad (59)$$

$$M_K(\mathbf{c}) = \frac{e^{(f_- - f_+)\tau}}{K} \sum_{i=1}^K \left(\frac{f_+}{f_-} \right)^{c_i} \quad (60)$$

$$\mathbb{E}_q[M_K] = e^{(f_- - f_+)\tau} \mathbb{E}_q \left[\left(\frac{f_+}{f_-} \right)^{c_i} \right] \quad (61)$$

$$= e^{(f_- - f_+)\tau} \exp \left(f_- \tau \left(\frac{f_+}{f_-} - 1 \right) \right) = 1 \quad (62)$$

$M_K \rightarrow 1$ and $D_{KL}(p(\mathbf{c})||q(\mathbf{c})) \rightarrow 0$

Thus in the limit of a large number of neurons $K > 1$, the exact mutual information approaches its theoretical upper bound

$$D_{KL}(p_+(c)||p_-(c)) = \frac{1}{\log(2)} \left(f_+ \tau \left(\log \left(\frac{f_+}{f_-} \right) - 1 \right) + f_- \tau \right) \quad (63)$$

which only depends on the boundary values of the individual neurons firing rates. Notice that we can generalize the above reasoning to neurons with tuning curves $f_i(s)$ defined over the interval S_i as $f_i(s) = f(K(s - s_{-,i}))$, where f is smoothly varying over $(0, s_+ - s_-)$ and within the range firing range (f_-, f_+) . Following the same steps as above yields a new theoretical upper bound

$$\frac{1}{s_+ - s_-} \int_0^{s_+ - s_-} f(s) \tau \left(\log_2 \left(\frac{f(s)}{f_-} \right) - 1 \right) ds + f_- \tau. \quad (64)$$

This integral bound is always smaller than the theoretical bound $D_{KL}(p_+(c)||p_-(c))$ attained for a discontinuous step-wise tuning curve, confirming the optimality of the bang-bang strategy in the limit of a large number of independent Poissonian encoding units.

2.2 Population size and stimulus dynamics

$$I(\mathbf{c}, s) = -\mathbb{E}_p \left[\log_2 \left(\frac{1}{K} \sum_{i=1}^K \left(\frac{f_+}{f_-} \right)^{c_i} \right) \right] + f_+ \log_2 \left(\frac{f_+}{f_-} \right) \quad (65)$$

$f_+ \leftarrow f_+/K, f_- \leftarrow f_-/K$ and $\tau \leftarrow \tau/K^2$

2.3 Tuning curves redundancy

2.4 Crossover to the Fisher information regime

$$I(\mathbf{c}, s) = \int_{s_-}^{s_+} ds p(s) D_{KL}(p(\mathbf{c}) \| p(\mathbf{c}|s)) \quad (66)$$

$$D_{KL}(p(\mathbf{c}) \| p(\mathbf{c}|s)) = -\mathbb{E} \left[\log_2 \left(\right) \right] \quad (67)$$

$$I(\mathbf{c}, s) = \frac{1}{M} \sum_{m=1}^M D_{KL}(p(\mathbf{c}) \| p(\mathbf{c}|s = m)) \quad (68)$$

$$D_{KL}(p(\mathbf{c}) \| p(\mathbf{c}|s = m)) = -\mathbb{E} \left[\log_2 \left(\frac{1}{M} \sum_{l=1}^M Q_l^m(\mathbf{c}) \right) \right] \quad (69)$$

$$Q_m^l(\mathbf{c}) = \prod_{k=1}^K \left(\frac{f_k(l)}{f_k(m)} \right)^{c_k} e^{f_k(l) - f_k(m)} \quad (70)$$

$$\frac{\partial I(\mathbf{c}, s)}{\partial f(i)} = \frac{1}{M} \sum_{m=1}^M \quad (71)$$

Sanov's theorem, multivariate case, non-Poissonian neurons