The role of stimulus parameterization in neural information and coding accuracy

(Forschungszentrum Jülich, April 1st, 2026)

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Motivation – Outline

Stimulus intensity, as a physical quantity, can be equivalently described in different unit systems. (Pa, dB, W/m^2)

Consequences? Reference-frame invariance?

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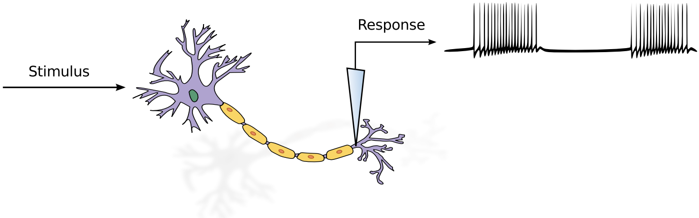
Stimulus intensity, as a physical quantity, can be equivalently described in different unit systems. (Pa, dB, W/m^2)

Consequences? Reference-frame invariance?

1. Fisher information (coding accuracy)
   - 'Adaptation' of neural coding accuracy
   - Psychophysical stimulus scale (*auditory nerve*)
2. Mutual information (*stimulus-specific* information)
   - Unique decomposition?
   - Example: auditory nerve

Information measures and neurons (informal)

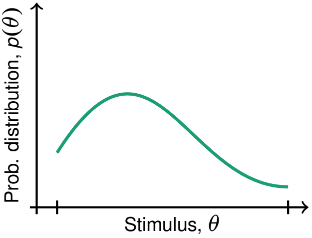
- Neural coding: How neurons (populations) encode and process information about their environment?



- *Indirect:* degree to which the response reflects the stimulus

1. Coding precision: the accuracy of stimulus identification
   Fisher information (Cramér-Rao bound):
   Paradiso (1988), Stemmler (1996), Abbott & Dayan (1999), Greenwood *et al.*
2. "How much information?" (stimulus→response)
   Mutual information (bits)
   MacKay & McCulloch (1952), Stein (1967), Laughlin (1981), Bialek *et al.*, ...

Neuronal coding accuracy and stimulus distribution



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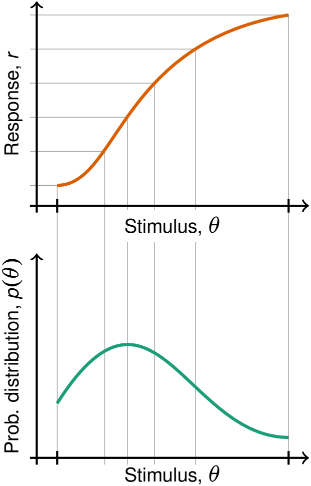

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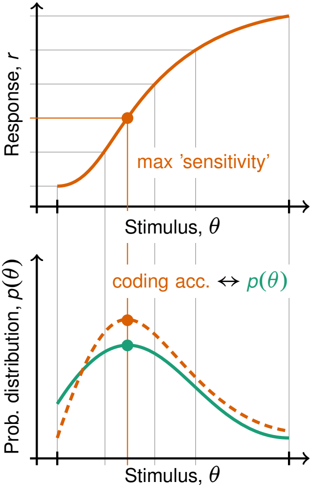


Neuronal coding accuracy and stimulus distribution

Optimal stimulation (peak coding accuracy):

– stochastic models
Lansky & Greenwood, *Neural Comput.* (2005); . . .

– auditory system
Jenison & Reale, *Netw. Comput. Neural Syst.* (2003)

Stimulus probability *vs.* coding accuracy:
(*efficient coding hypothesis*)

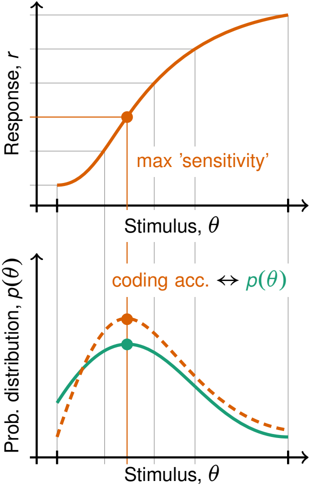
– sound intensity
Dean *et al.*, *Nat. Neurosci.* (2005); Watkins & Barbour, *Nat. Neurosci., Cereb. Cortex.* (2008, 2011), . . .

– interaural level differences
Dahmen *et al.*, *Neuron* (2010)

– interaural time differences
Maier *et al.*, *J. Neurophysiol.* (2012)

– primary visual cortex
Durant *et al.*, *J. Opt. Soc. Am. A* (2007)

– somatosensory cortex
Garcia-Lazaro *et al.*, *Eur. J. Neurosci.* (2007)



Cramér-Rao bound and Fisher information

- Electrophysiological experiment: stimulus, $\theta \rightarrow$ response, r
- Repeated trials (single neuron $\times$ population): response variability
- Stimulus-response model: $R \sim f(r|\theta)$ (θ continuously varying)
- *How precisely can we estimate given θ from the observed r?*

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- Stimulus-response model: $R \sim f(r|\theta)$ (θ continuously varying)
- *How precisely can we estimate given θ from the observed r?*
- For any *unbiased* estimator $\hat{\theta}(r)$ ($\mathrm{E}_{R|\theta}\,\hat{\theta}(R) = \theta$)

Cramér-Rao bound: $$\mathrm{MSE}(\theta) \geq \frac{1}{J(\theta)}$$

Fisher information: $$J(\theta) = \int \left[\frac{\partial \log f(r|\theta)}{\partial \theta}\right]^2 f(r|\theta)\,\mathrm{d}r$$

- Asymptotic theory: n i.i.d. samples $\sim f(r|\theta)$, then there exists $\hat{\theta}_n$: $\sqrt{n}(\hat{\theta}_n - \theta) \to N\big(0, 1/J(\theta)\big)$

$$\mathrm{MSE}_n(\theta) \geq \frac{1}{nJ(\theta)}$$ tight for large n or SNR

Parameterization of the stimulus

- Stimulus θ *equivalently* evaluated in different measurement units

$$\lambda = \varphi(\theta), \qquad \theta \in [\theta_{\mathrm{min}}, \theta_{\mathrm{max}}]$$

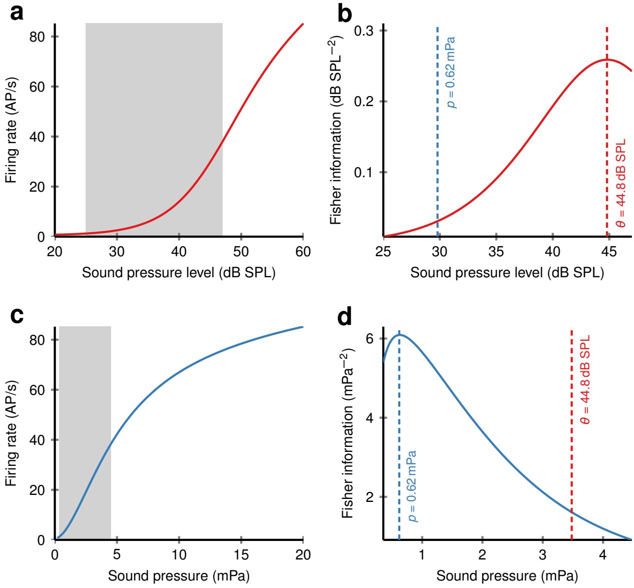
- φ regular (strictly increasing and $\mathcal{C}^1$): $\theta_1 > \theta_2 \Rightarrow \varphi(\theta_1) > \varphi(\theta_2)$
  – sound: intensity (W/m^2) *vs.* pressure (Pa) *vs.* level (dB SPL)
- Models $f(r|\theta)$ and $f(r|\lambda)$ are equally 'good' (φ bijective)
- Fisher information and stimulus distr. in different reference frames

$$J_\lambda(\lambda) = \left(\frac{\mathrm{d}\varphi^{-1}(\lambda)}{\mathrm{d}\lambda}\right)^2 J_\theta\big(\varphi^{-1}(\lambda)\big),$$

$$p_\lambda(\lambda) = p_\theta\big(\varphi^{-1}(\lambda)\big)\,\frac{\mathrm{d}\varphi^{-1}(\lambda)}{\mathrm{d}\lambda}.$$

Example: auditory neuron

(Winslow & Sachs, *Hear. Res.*, 1988)



(Kostal & Lansky, *Neural Comput.*, 2015)

Re-parameterization for given $f(r;\theta)$ and $p_\theta(\theta)$

- Under mild conditions there exists a regular φ:
  Thm. **1**: the profile of $J(\cdot)$
  Thm. **2**: the 'peak matching' $J(\cdot) \leftrightarrow p(\cdot)$
  are **arbitrary**

Kostal, *J. Math. Psychol.* (2016)

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1. For 'any' $g(\lambda) > 0, \lambda \in [0,1]$ there exists $a > 0$:

$$\frac{\mathrm{d}\varphi(\theta)}{\mathrm{d}\theta}\sqrt{ag\big(\varphi(\theta)\big)} = \sqrt{J_\theta(\theta)} \quad \Rightarrow \quad J_\lambda(\lambda) = ag(\lambda)$$

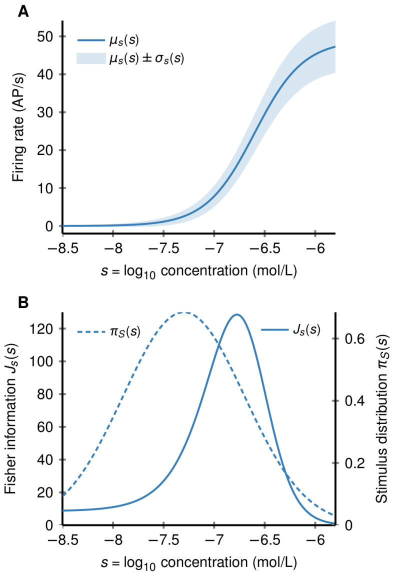
2. For 'any' $h(\cdot) > 0$, $\quad h(x) \not\propto x^2$

$$\left(\frac{\mathrm{d}\varphi(\theta)}{\mathrm{d}\theta}\right)^2 h\left(p_\theta(\theta)\left|\frac{\mathrm{d}\varphi(\theta)}{\mathrm{d}\theta}\right|^{-1}\right) = J_\theta(\theta) \;\Rightarrow\; J_\lambda(\lambda) = h\big(p_\lambda(\lambda)\big)$$

Exception: Jeffreys prior $p_\theta(\theta) \propto \sqrt{J_\theta(\theta)}$ is invariant.

Example: olfactory receptor neuron

(Rospars *et al.*, *J. Neurosci.*, 2008)



- Stimulus s: log-concentration
- Response: AP/s, sigmoid+noise
- Stimulus distribution $\pi_S \not\leftrightarrow J_s$!
- Exists $x = \varphi(s) : \pi_X(x) = J_x(x)$?

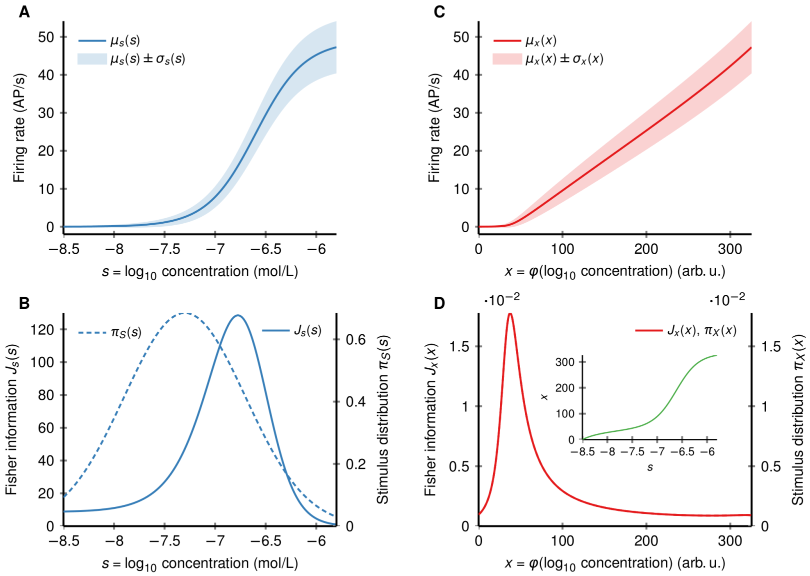
YES:

- Apply *Thm.* **2** for: $h(z) = z$
- Then

$$x = \varphi(s) = \int_{s_{\min}}^{s} \frac{J_s(z)}{\pi_s(z)}\, \mathrm{d}z$$

Example: olfactory receptor neuron

(Rospars *et al.*, *J. Neurosci.*, 2008)



Stimulus unit based on the perception intensity

- Interpretation of $J(\theta)$ is *inseparable* from the choice of units.
- Too many 'equivalent' scales. *Is there a special one?*

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- Interpretation of $J(\theta)$ is *inseparable* from the choice of units.
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1. Assume psychophysical function: $S(\theta)$ (S: perceptual intensity)
2. Propose stimulus scale $S(\lambda) = c\lambda$ (*Fechner:* $S \propto \log\theta,\ c > 0$)
3. *Why?*
4. *Just-noticeable difference* (JND) ΔS depends on $\Delta\lambda$, not on λ.
   (Equiv.: JND-inducing $\Delta\lambda$ does not depend on λ.)
5. Ideal observer approx.: $\Delta\lambda = D_\alpha / \sqrt{J_\lambda(\lambda)} \Rightarrow J_\lambda(\lambda) = \text{const.}$
6. Assuming the *matching*: $J_\lambda \propto p_\lambda \Rightarrow p_\lambda(\lambda) = \text{const.}$
7. By Thm. 2: in the original θ it *must* be $p_\theta \propto \sqrt{J_\theta}$.
8. Hence
$$\lambda = \varphi(\theta) = \int_{\theta_{\min}}^{\theta} \sqrt{J_\theta(z)}\,\mathrm{d}z.$$

Sound intensity as the stimulus parameter

- Sound 'loudness': (acoustic) pressure p (Pa)?
- Sound intensity I (W/m^2) and air sound pressure level L (dB SPL)

$$I = \frac{p^2}{Z}, \qquad\qquad L = 20 \log_{10} \frac{p}{p_0}$$

$(Z \doteq 400\,\mathrm{N} \cdot \mathrm{s} \cdot \mathrm{m}^{-3}, \quad p_0 = 20\,\mu\mathrm{Pa})$

- *Note:* Fechner law for 'intensity' $I \Rightarrow S \propto L$, but ...

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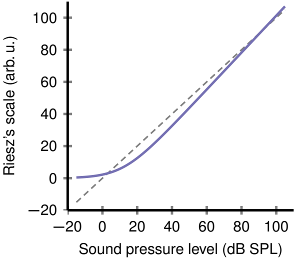
- Riesz's psychophysical function (pure tones)

$$S(p) = \frac{\log[(S_0 - S_\infty)p_0^{2\varrho} + S_\infty p^{2\varrho}]}{S_\infty \varrho} + C,$$

Riesz, *Phys. Rev.* (1928)

Coding accuracy on the psychophysical stimulus scale

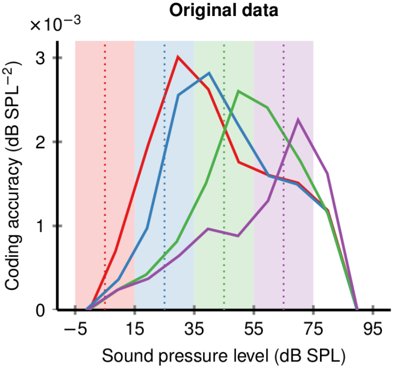
- $S \Rightarrow$ Riesz's scale for sound intensity: $\lambda \propto S$
- *Relevance of* λ *?* (non-human subjects)
- $S \propto \log(\theta^k + c)$, $k \approx 1$: long history (*mel* scale for frequency, ...)
  Norwich & Wong, *Percept. Psychophys.* (1997)



- Neurons in the auditory system adjust their rate-level functions to improve coding accuracy (J) over high-probability stimulus regions
  Dean *et al.*, *Nat. Neurosci.* (2005); Watkins & Barbour, *Nat. Neurosci.* (2008), ...
- D. Barbour: primary auditory cortex of *marmoset monkey*
- Sound level distribution $p(L)$ (matching the characteristic freq.):
  - uniform over -15 dB SPL to 105 dB SPL,
  - +20 dB-wide plateau of high-probability stimulus region
  - pure tone sample every 100 ms

Experimental data example

- Peak coding accuracy does not align with frequent low sound intensities
- Transform both $J(L)$ and $p(L)$ from dB SPL to Riesz's scale



Original data from Watkins & Barbour, *Nat. Neurosci.* (2008)

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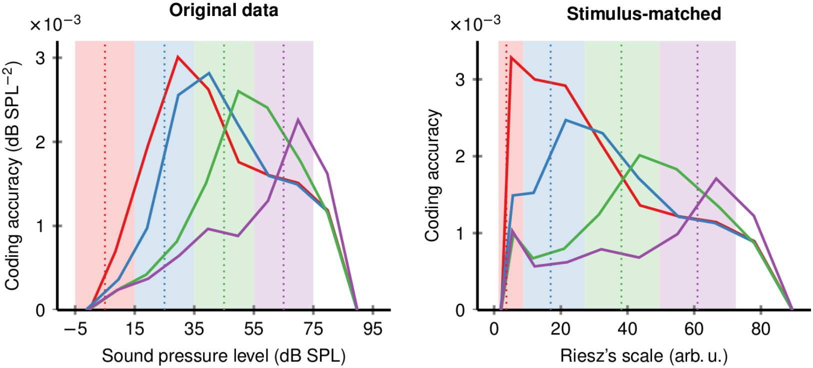

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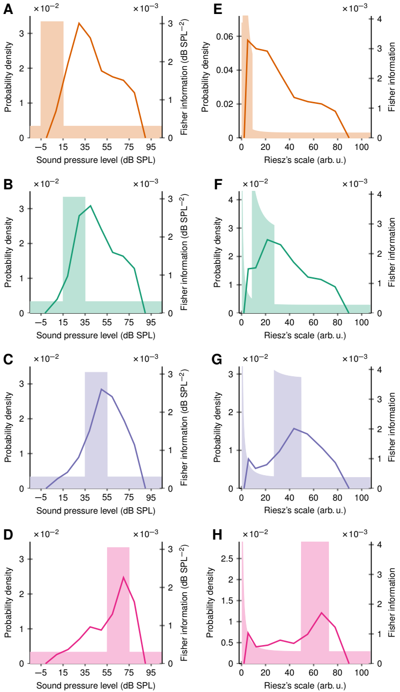
More details: Kostal, *J. Math. Psych.*, *Sci Rep.* 2016, 2017


A
B
C
D
E
F
G
H
Probability density
Fisher information (dB SPL^{-2})
Sound pressure level (dB SPL)
Fisher information
Riesz's scale (arb. u.)
×10^{-2}
×10^{-3}

"How much information": Mutual information

- Stimulus (intensity): $s \in \mathcal{S}$ (cont.), random variable $S \sim p_S(s)$
- Response (firing rate, ...): $r \in \mathcal{R}$, stochastic: $f_{R|S}(r|S = s)$

$$p_R(r) = \int_{\mathcal{S}} f_{R|S}(r|s) p_S(s) \, \mathrm{d}s$$

- Mutual information (joint p.d.f. $f_{S,R}(s,r) = f_{R|S}(r|s)p_S(s)$)

$$I(S;R) = \int_{\mathcal{S}} \int_{\mathcal{R}} f_{S,R}(s,r) \ln \frac{f_{S,R}(s,r)}{p_S(s)p_R(r)} \, \mathrm{d}r \, \mathrm{d}s$$

- $I(S;R)$: maximum information that can be communicated *reliably* by neuronal 'model' $f_{R|S}$ subject to the input statistics p_S.

Stimulus-specific information

- Stimulus-specific information: $i(S = s; R)$ such that

$$\boxed{I(S;R) = \int_{\mathcal{S}} i(s;R) p_S(s)\,\mathrm{d}s}$$

- Decomposition not unique, options (e.g.):

(DeWeese & Meister (1999), Bezzi (2007), Wibral *et al.* (2015), . . .)

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1. Difference of entropies, $h(R) = -\int_{\mathcal{R}} p_R(r) \log p_R(r)\, \mathrm{d}r$

$$i_h(s;R) = h(R) - h(R|s)$$

2. Specific surprise (Kullback-Leibler divergence)

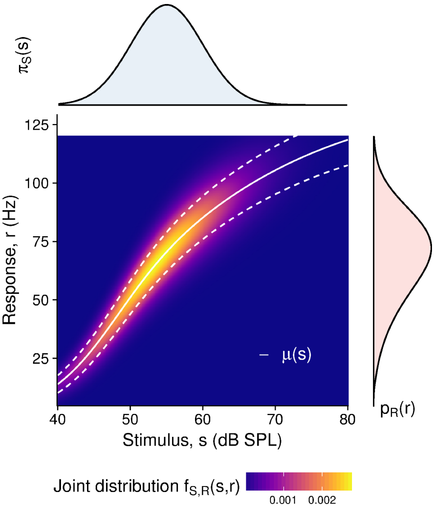
$$i_{\mathrm{KL}}(s;R) = \int_{\mathcal{R}} f_{R|S}(r|s) \log \frac{f_{R|S}(r|s)}{p_R(r)}\, \mathrm{d}r.$$

3. Specific information (Dan Butts, 2003)

$$i_{\mathrm{ssi}}(s;R) = \int_{\mathcal{R}} i_h(r;S) f_{R|S}(r|s)\, \mathrm{d}r$$

(+ any weighted combination of 1, 2, 3; $i_h \neq i_{\mathrm{KL}} \neq i_{\mathrm{ssi}}$)

Example: auditory nerve



$f_{R|S}$: cat auditory nerve fiber best responding to 8 kHz pure tones
(Winslow & Sachs, *Hearing Res.*,1988)

- Stimulus: intensity (dB SPL)
  π_S: (Wen *et al.*, 2009)
- Response: firing rate (Hz)

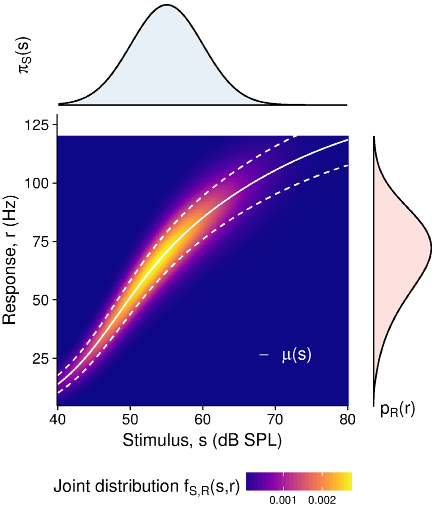
$I(S; R) \doteq 1.2$ bit

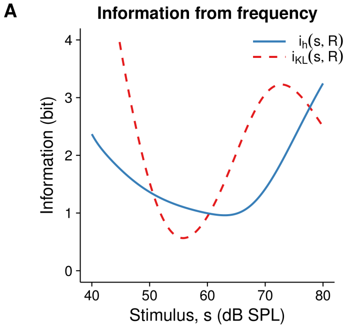
Consider $(s, r) \to (x, y)$:

$$x = s, \qquad y = 1/r$$

and compare $i_h, i_{\mathrm{KL}}, \ldots$

Example: auditory nerve





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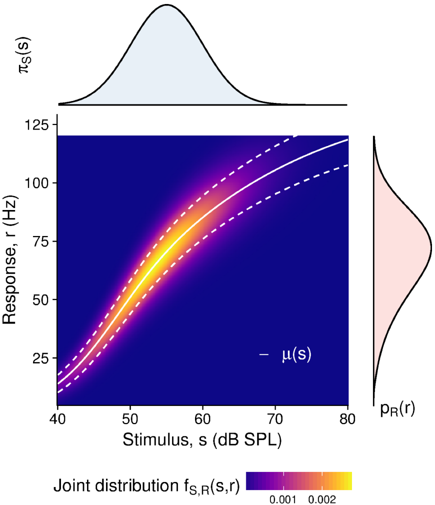

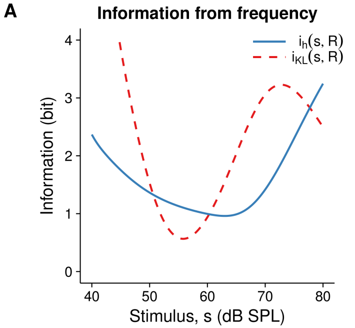

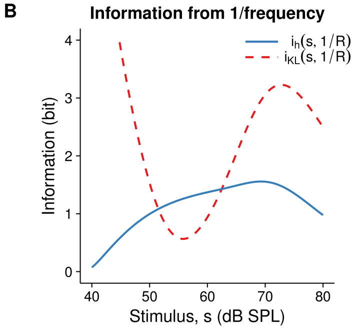

Stimulus-specific information: invariance

- Invariance: $i\big(\varphi(s); \xi(R)\big) = i(s; R)$?

$$i_h(s; R) = h(R) - h(R|s)$$

$$i_{\mathrm{KL}}(s; R) = \int_{\mathcal{R}} f_R(r|s) \ln \frac{f_R(r|s)}{p_R(r)} \,\mathrm{d}r$$

$$i_{\mathrm{ssi}}(s; R) = \int_{\mathcal{R}} i_h(r; S) f_R(r|s) \,\mathrm{d}r$$

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$$i_{\mathrm{ssi}}(s;R) = \int_{\mathcal{R}} i_h(r;S) f_R(r|s) \, \mathrm{d}r \qquad ✘$$

$$\textit{e.g.,} \;\; i_h\big(\varphi(s);\xi(R)\big) = i_h(s;R) + \int_{\mathcal{R}} \ln \left|\xi'(r)\right| \big(p_R(r) - f_R(r|s)\big) \, \mathrm{d}r$$

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$$i_{\mathrm{ssi}}(s;R) = \int_{\mathcal{R}} i_h(r;S) f_R(r|s)\, \mathrm{d}r \qquad ✘$$

- Is i_{KL} the only invariant measure? No.

$$i_n(s_n;R) = \int i_{\mathrm{KL}}(s_0;R) \prod_{i=0}^{n-1} f_{R|S}(r_i|s_{i+1}) f_{S|R}(s_i|r_i)\, \mathrm{d}s_i\, \mathrm{d}r_i, \quad n \geq 1$$

- But i_{KL} is unique (invariant) in a 'reasonably' general class ($i_h, i_{\mathrm{ssi}}, \ldots$),

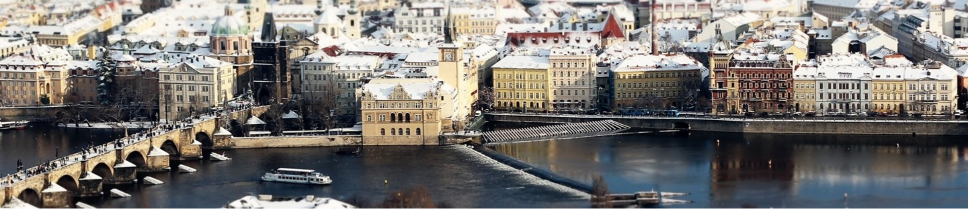
$$\text{e.g.,}, \quad i(s;R) = \int_{\mathcal{R}} g\Big(p_S, f_{R|S}, p_R\Big)\, \mathrm{d}r$$

More details: Kostal & D'Onofrio, *Biol. Cybern.* 2018

Work in progress ...

- Stimulus-specific information:
  - The p_S-dependence cannot be removed ...
  - *But:* Can we propose a meaningful decomposition into "*channel-only*" and "*input-specific*" parts?

    Ongoing collab. with Giuseppe D'Onofrio
- General statistical methodology:
  - Estimation: MAP, MMSE, ML(Bayesian), ML(Frequentist)
  - Correlation measures: Pearson *vs.* Spearman
  - Tests? (Wald, ...)



Conclusions

1. Fisher information and model parameterization: ambiguity,
   – relevance of the *chosen* stimulus scale should be considered
2. Matching coding accuracy to the stimulus distribution:
   – neurophysiological *vs.* 'methodological' explanation
3. Psychophysical function – experimental data *vs.* approximations
4. Stimulus-specific information: invariant options

- **Thanks to**: *Petr Lansky*, Dennis Barbour, Peter Latham, Giuseppe D'Onofrio

Asymptotic theory

- *Problem*: CR bound achievability and bias $b(\theta) = m(\theta) - \theta$
- Restrict to mean squared error $\text{MSE}(\theta)$ of unbiased estimators

$$\text{MSE}(\theta) \geq \frac{1}{J(\theta)} \qquad \text{since } \text{MSE}(\theta) = \text{Var}\,\hat{\theta}(R) + b^2(\theta)$$

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- Assume i.i.d. case: $f(r_1, \ldots, r_n; \theta) = \prod_{i=1}^{n} f(r_i; \theta)$
- As $n \to \infty$ there exists $\hat{\theta}_n$: $\sqrt{n}(\hat{\theta}_n - \theta) \to N\big(0, 1/J(\theta)\big)$

$$\mathrm{MSE}_n^2(\theta) \geq \frac{1}{nJ(\theta)} \qquad \text{tight for large } n$$

(Kostal *et al.*, *J. Neural Eng.*, 2005)

- More general $f(r_1, \ldots, r_n; \theta)$: CR bound *vs.* asymptotics of $\hat{\theta}_n$?
  LAN: Greenwood *et al.*, *Phys. Rev. E* **60** (1999)

Additional properties of i_{KL}

- Let $I[p_S] \equiv I(S;R)$, and $p_S \in \mathcal{F}$ convex & compact, directional ($g \in \mathcal{F}$) derivative ('weak', 'Gateaux', ...)

$$\delta_g I[p_S] = \lim_{\varepsilon \downarrow 0} \frac{I[(1-\varepsilon)p_S + \varepsilon g] - I[p_S]}{\varepsilon},$$

1. Sensitivity of MI to a change in prob. of $S \in [s, s + \mathrm{d}s]$.

$$I[(1-\varepsilon)p_S + \varepsilon g] \doteq (1-\varepsilon) I[p_S] + \varepsilon \int_{\mathcal{S}} g(s)\, i_{\mathrm{KL}}(s;R)\, \mathrm{d}s,$$

2. Optimization (capacity) $C = I[\pi_0] = \max_{p_S \in \mathcal{F}} I[p_S]$

$$i_{\mathrm{KL}}(s;R) \le C, \qquad \text{eq. iff} \quad s : p_S(s) > 0$$

- Note that

$$i_{\mathrm{KL}}(\{s_1, s_2\}; R) \neq i_{\mathrm{KL}}(s_1; R) + i_{\mathrm{KL}}(s_2 | s_1; R)$$

hovewer: $i_{\mathrm{KL}}(s; \{R_1, R_2\}) = i_{\mathrm{KL}}(s; R_1) + i_{\mathrm{KL}}(s; R_2 | R_1)$