Bits from brains for biologically inspired computing

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(Presented by Sten Sootla)

Why information theory in neuroscience?

- Marr’s 3 levels of information processing: **task**, **algorithmic** and **implementation** levels.
- Shortcoming: results obtained at any of the levels does not constrain the possibilities at any other level.
- Missing relationships between Marr’s levels can be filled by **information theory**:
    1. implementation <-> task
    2. implementation <-> algorithmic

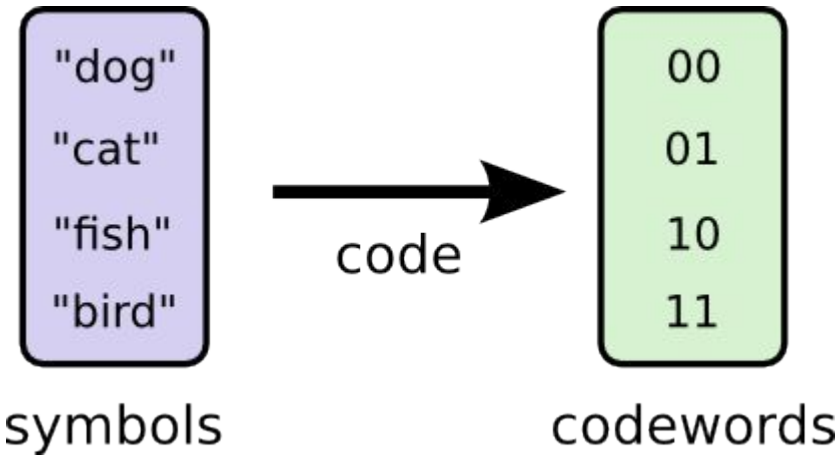
Information theory basics

Motivating example: how much the response of a neuron varies across stimuli?

Entropy

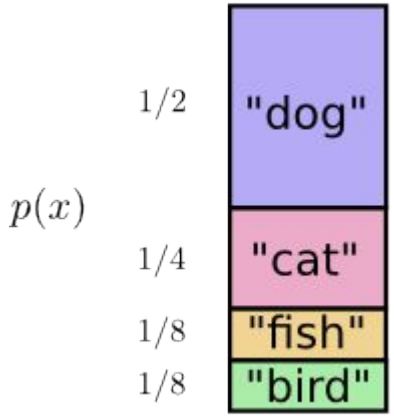
- Your friend Bob can only speak 4 words.
- He lives in Australia and you'd like to talk to him using as few bits as possible, because every bit costs money.

- You design a **fixed-length** code:

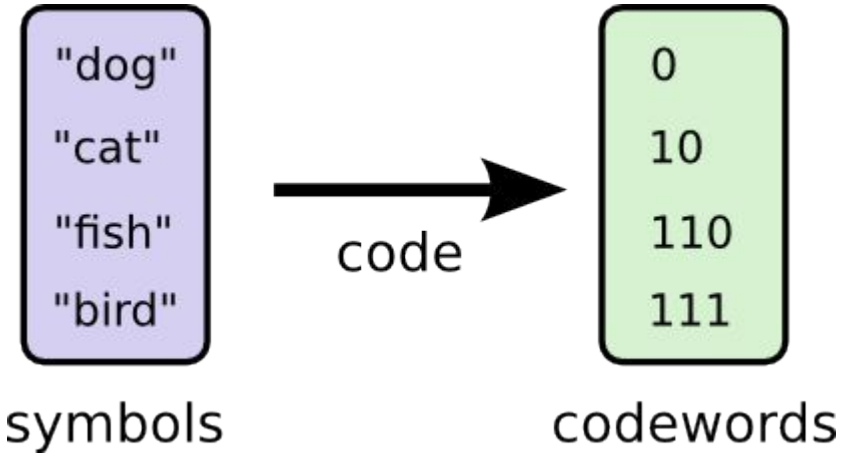


Entropy

- However, you notice that Bob doesn't use every word equally often:



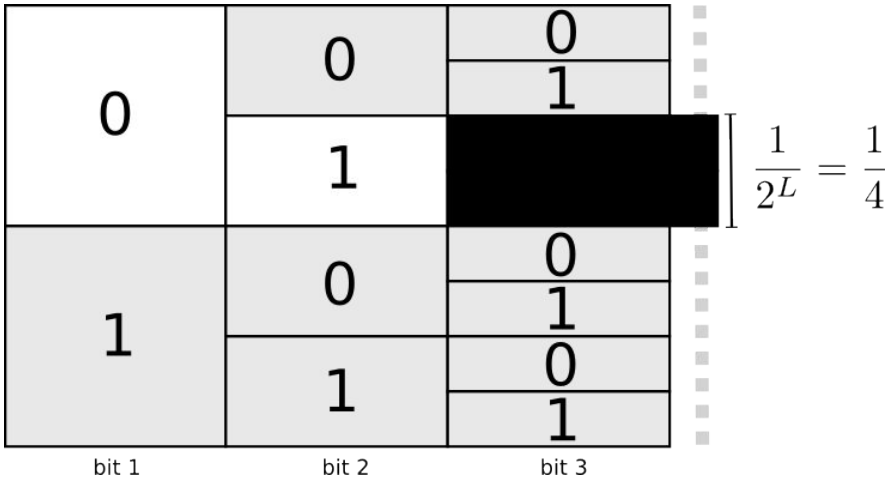
- So you design a clever **variable-length** code that uses this information:



Entropy

- Since you now use a variable length code, the codewords can’t start with a common prefix. Otherwise it would be **impossible to decipher the code**.
- So by choosing a code, you make a sacrifice from the space of all possible codewords.

- Choosing the code “01”, you sacrifice ¼ of all possible codes:



Entropy

- The **optimal** way to encode the information is to distribute our “budget” in proportion to how common an event is.
- The average message length using the optimal code is called **entropy**:

$$H(R) = \sum_{r \in R} p(r) \log_2 \frac{1}{p(r)}.$$

- Another interpretation: the **amount of uncertainty** one has about a random variable.

Conditional entropy

- Neurons are noisy - their responses to repetitions of identical stimulus differ across trials.
- To quantify the noise, we use **conditional entropy**:

$$H(R|S) = \sum_{s \in S} p(s) \sum_{r \in R} p(r|s) log_2 \frac{1}{p(r|s)}.$$

- The noisier the neuron, the greater the $H(R|S)$.

Mutual information

- How much of the information capacity in neural activity is robust to noise?
- To quantify it, we use **mutual information:**

$$I(S:R) = \sum_{s,r} p(s,r) log_2 \frac{p(s,r)}{p(s)p(r)} = H(R) - H(R|S).$$

- It's the **reduction in the uncertainty** of R due to the knowledge of S.

Kullback-Leibler distance

- It measures the “distance” between 2 distributions:

$$D_{KL}(p||q) = \sum_{x \in X} p(x) \log_2 \frac{p(x)}{q(x)}.$$

- A measure of inefficiency of assuming that distribution is *q* when the true distribution is *p*.
- Mutual information is just a **special case** of this: the KL-distance between the joint distribution *p(x,y)* and the product distribution *p(x)p(y)*.

Local information theoretic quantities

- We have looked at **average** information content of random variables.
- We can also study **local** information theoretic quantities, which allow us to quantify information in a **single realization** of a random variable.
- Localized measures are trivially obtained by omitting the expectation over the whole distribution.
- For example:

$$i(s:r) = \log_2 \frac{p(s,r)}{p(s)p(r)}.$$

Analyzing neural codings

Crossing the bridge between the task level and implementation level.

Which neural responses carry information about which stimuli?

- Can be easily answered by computing **I(S:R)**.

- Example: we could extract features $F_i(R)$ from neural responses: time of the first spike and firing rate, and calculate $I(S:F_1(R))$ and $I(S:F_2(R))$.

How much does an observer of specific neural response change its beliefs about the identity of stimulus from p(s) to p(s|r)?

- Kullback-Leibler distance between *p(s)* and *p(s|r)*.
- ***Specific surprise***:

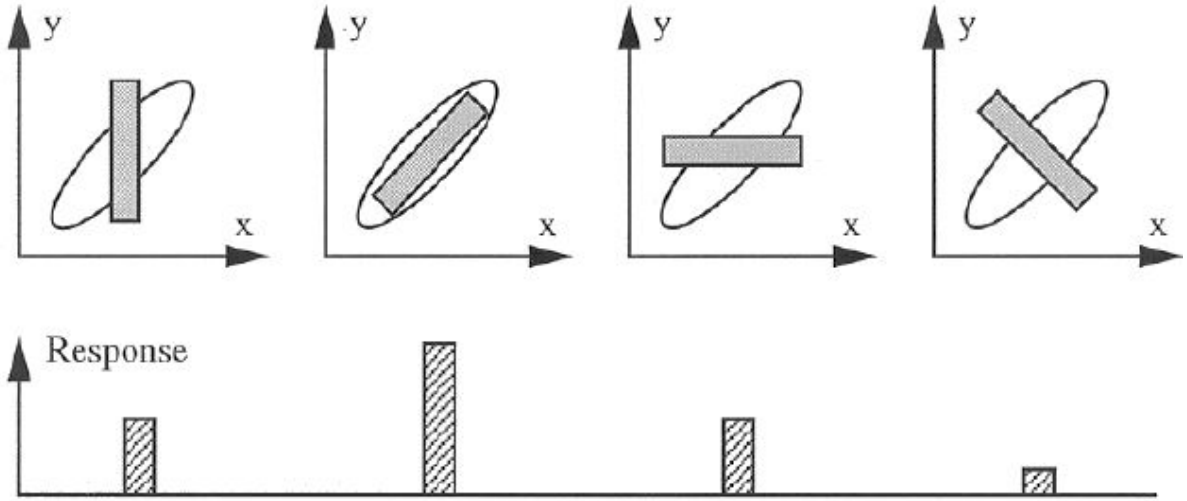
$$i_{sp}(S:r) = \sum_{s \in S} p(s|r) log_2 \frac{p(s|r)}{p(s)}.$$

- i_{sp} is a valid partition of mutual information into more specific, response dependent contributions, since:

$$I(S:R) = \sum_{r \in R} p(r) i_{sp}(S:r).$$

Motivating example

1. How to quantify the **reduction in uncertainty** about the stimulus gained by a particular response *r*?
2. Which stimulus is reliably associated with the responses that are relatively unique for that stimulus?



How to quantify the reduction in uncertainty about the stimulus gained by a particular response r?

- "In contrast to the previous question, here we ask whether the response increases or reduces uncertainty about the stimulus."
- ***Response-specific information***:

$$i_r(S:r) = H(S) - H(S|r).$$

- i_r is a valid partition of mutual-information:

$$I(S:R) = \sum_{r \in R} p(r) i_r(S:r).$$

Which stimulus leads to responses that are informative about the stimulus itself?

- Response is informative if it has a large $i_r(S:r)$.
- We then ask how informative the responses for a given stimulus are on average over all responses that the stimulus elicits with probabilities p(r|s).
- We obtain the ***stimulus specific information***:

$$i_{SSI}(s:R) = \sum_{r \in R} p(r|s) i_r(S:r).$$

- i_{SSI} is a valid partition mutual information:

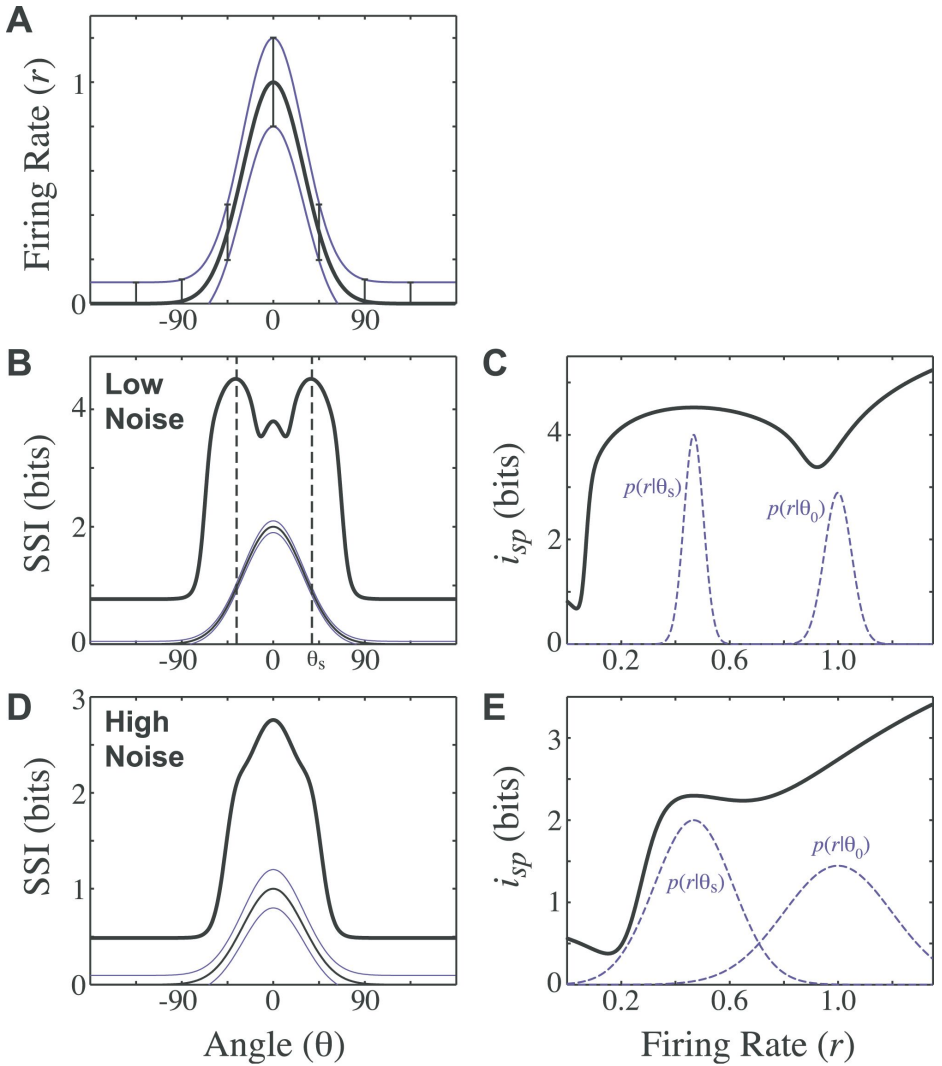
$$I(S:R) = \sum_{s \in S} p(s) i_{SSI}(s:R).$$

Specific example

- Two competing interpretations:
  1. The stimuli that evoke the **highest firing rates** are most important to the neuron.
  2. Nearby stimuli are most easily discriminated in **high-slope regions** of the tuning curve.

- Both interpretations are correct, depending on the amount of neuronal variability (noise).

(Tuning curves, Neuronal Variability and Sensory Coding. 2006. Daniel A. Butts, Mark. S. Goldman.)



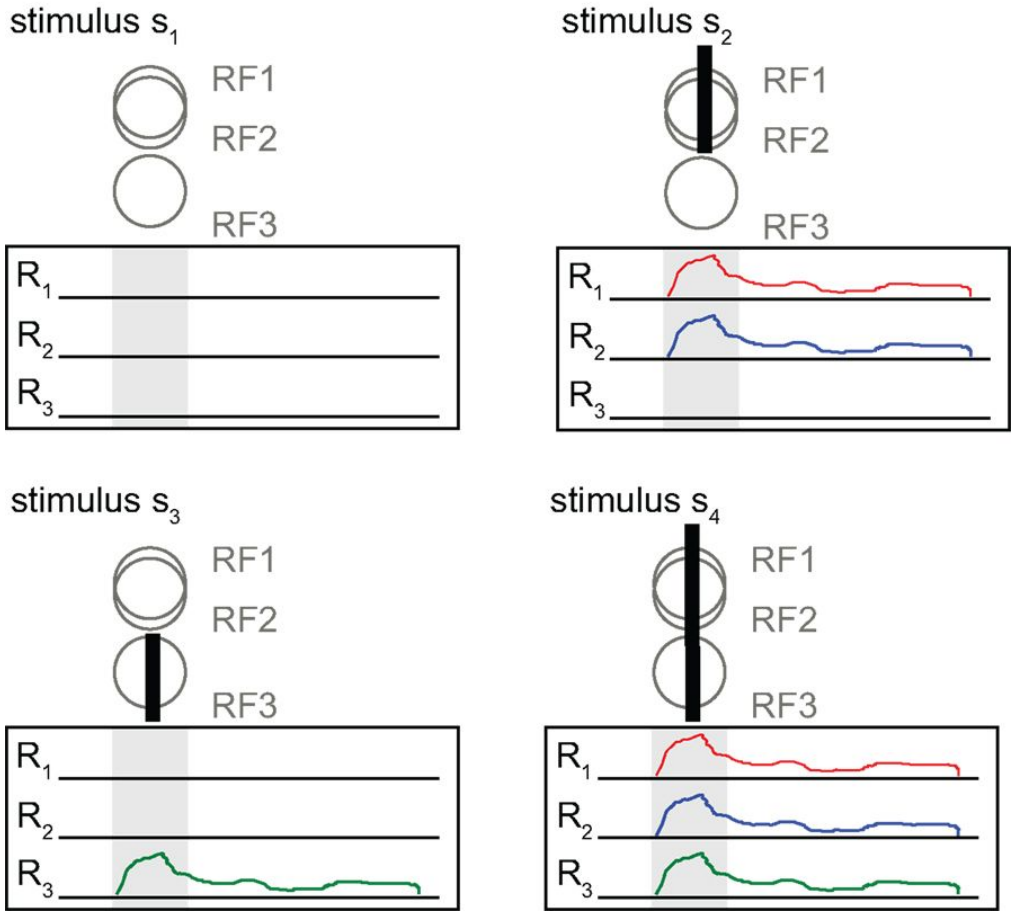
Relevance to BICS: “Encoding of an environment in a computing system may be modeled on that of a neural system that successfully lives in the same environment.”

Partial information decomposition

Motivating example: How is information about a stimulus distributed in the brain between the neurons?

Intuition

- $H(S) = 2$
- $H(R_i) = 1$
- $I(S:R_1,R_2,R_3) = 2$
- $I(S:R_i) = 1$ (!)
- **Redundancy** - neurons 1,2 show identical responses
- **Synergy** - how much information neurons 1,3 have about a single short bar?
- **Unique information** - consider neurons 1,3 and stimuli 1,3



Mathematical formulation

- Let's consider input variables R_1 and R_2 and an output variable S. Then we can decompose:

$$I(S : R_1) = SI(S : R_1; R_2) + UI(S : R_1 \setminus R_2),$$

$$I(S : R_2) = SI(S : R_2; R_1) + UI(S : R_2 \setminus R_1),$$

$$I(S : R_1, R_2) = UI(S : R_1 \setminus R_2) + UI(S : R_2 \setminus R_1) + SI(S : R_1; R_2) + CI(S : R_1; R_2).$$

- Only **one** of the terms needs to be defined!

Proposed axioms for redundant information

- **Symmetry**: the redundant information that variables $R_1, R_2, \ldots, R_n$ have about S is symmetric under permutations of $R_1, R_2, \ldots, R_n$.
- **Self-redundancy**: the redundant information that R_1 shares with itself about S is the mutual information $I(S:R1)$.
- **Monotonicity**: the redundant information that variables $R_1, R_2, \ldots, R_n$ have about S is smaller than or equal to the redundant information that variables $R_1, R_2, \ldots, R_{n-1}$ have about S.

Mathematical formulation

- Additional assumption: **unique information** should depend only on the **marginal distributions** $P(s,r_1)$ and $P(s,r_2)$.
- So we can define:

$$\tilde{UI}(S : R_1 \setminus R_2) = \min_{Q \in \Delta_p} I_Q(S : R_1 | R_2),$$

where $\Delta_p = \{Q \in \Delta : Q(S = s, R_1 = r_1) = P(S = s, R_1 = r_1)$ *and* $Q(S = s, R_2 = r_2) = P(S = s, R_2 = r_2)\ \forall s \in S, r_1 \in R_1, r_2 \in R_2\}$.

Mathematical formulation

- **Redundant information:**

$$\tilde{SI}(S : R_1; R_2) = \max_{Q \in \Delta_p} [I(S : R_1) - I_Q(S : R_1 | R_2)].$$

- **Shared information:**

$$\tilde{CI}(S : R_1; R_2) = I(S : R_1, R_2) - \min_{Q \in \Delta_p} I_Q(S : R_1, R_2).$$

- All these measures can be found by **convex optimization**, and they are **positive.**

Relevance to BICS: “Knowing how information is distributed over the agents can inform the designer of BICS about strategies to distribute the relevant information about a problem over the available agents.”

Example: reliability vs capacity.

Analyzing distributed computation in neural systems

Crossing the bridge between the implementation level and algorithmic level.

Motivation

- If we probe the system beyond early sensory or motor areas, we have little knowledge of what is actually encoded by the neurons in deeper inside the system.
- The gap between the task- and implementation level may become too wide.
- We may use information theory to link the **implementation** and **algorithmic** level, by retrieving a “footprint” of the information processing.

Partitioning of information processing

- Information **transfer** - how much information is transferred from source process to target process.
- Information **storage** - how much information in a process is predictable from its past.
- Information **modification** - quantifies the combination of information from various source processes into a new form that is not trivially predictable from any subset of these source processes.

State space reconstruction

- An optimal prediction of future realizations of a process typically requires looking at **many** past realizations of random variables of this process (pendulum example).
- A vector of past realizations, such that they're sufficient for prediction is a **state** of the system.
- Formally, we have to form the smallest collection of variables $\boldsymbol{X_t}=(X_t, X_{t1}, ..., X_{ti}, ...)$ with $t_i < t$ that jointly make X_{t+1} conditionally independent of all X_{tk} with $t_k < min(t_i)$:

$$p(x_{t+1}|x_{t_k}, \mathbf{x}_t) = p(x_{t+1}|\mathbf{x}_t).$$

1. Information transfer

- Information transfer from source process X to a target process Y:

$$TE(\mathbf{X}_{t-u} \to Y_t) = I(\mathbf{X}_{t-u} : Y_t | \mathbf{Y}_{t-1}) = H(Y_t | \mathbf{Y}_{t-1}) - H(Y_t | \mathbf{Y}_{t-1}, \mathbf{X}_{t-u})$$

- Interaction delay parameter need not be chosen *ad hoc*:

$$\delta = \underset{u}{\operatorname{argmax}} \left[TE(\mathbf{X}_{t-u} \to Y_t) \right]$$

- **Not** optimal for inference about **causal** interactions.

Problems with transfer entropy

In reality, we have more than 2 interacting processes.

1. **Common driver effect:**

$$\delta_{Z \to X} < \delta_{Z \to Y} \implies TE(\mathbf{X}_{t-u} \to Y_t) > 0$$

2. **Cascade effect:** if information if transferred from X to Y and then from Y to Z, bivariate analysis will also indicate information transfer from X to Z.

3. Two sources can transmit information **synergistically**.

2. Information storage

- We're concerned with **active** information storage (information stored in neural activity), not passive (synaptic weights):

$$A_{X_t} = \lim_{k \to \infty} I(\mathbf{X}_{t-1}^{k-} : X_t),$$

  where $X_t^{k-} = \{X_t, X_{t-1}, ..., X_{t-k+1}\}$.

- The limit can be replaced by finite k_{max}.

3. Information modification

- Information modification is an interaction between transmitted and/or stored information that results in modification of one of or the other.
- ***Local separable information***:

$$s_{X_t} = a_{X_t} + \sum_{\mathbf{z}_{t^-} \in \mathbf{V}_{X_t} \setminus \mathbf{X}_{t-1}} i(x_t : \mathbf{z}_{t^-} | x_{t-1}),$$

with $V_{X_t} \setminus X_{t-1} = \{\mathbf{Z}_{t^-}, ..., \mathbf{Z}_{t^-,G}\}$ indicating the set of G past state variables of all processes $\mathbf{Z}_{t^-,i}$ that transfer information into the target variable X_t .

Relevance to BICS: “These measures of how information is processed allow us to narrow in (derive constraints) on the algorithms being implemented in the neural system.”

Conclusion

- Neural system processing can be quantitatively partitioned into information **-storage**, **-transfer** and **-modification**. These observations allow us to derive constraints on possible neural algorithms.
- The **representation** that these algorithms operate on can be guessed by analyzing the neural codes.
- Care must be taken when analyzing neural codes because separation of how neurons code **uniquely**, **redundantly**, and **synergistically** has not been solved completely.