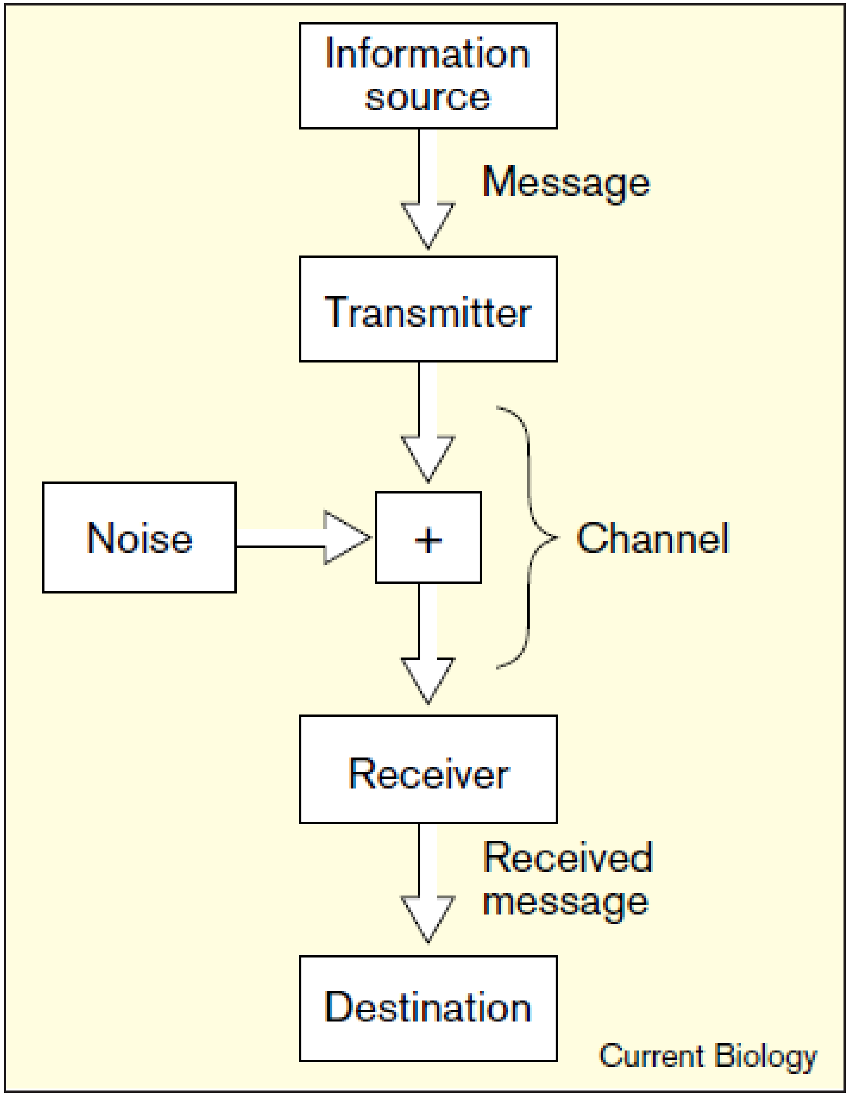
Information and neural computations

Why quantify information?

- We may want to know which feature of a spike train is most informative about a particular stimulus feature.
- We may want to know which feature of a stimulus a neural response is informative about.
- We may want know what information is gained by listening to groups of neurons rather than single neurons.
- We may want to compare the actual rate of information transmission with the theoretical maximum.

How we think about information



Stimulus

Response

Reinagel 2000 Current Biology 10:R542

Units of information

<u>1 bit</u> ≡ the amount of information in the answer to a yes-no question, where both answers are equally likely

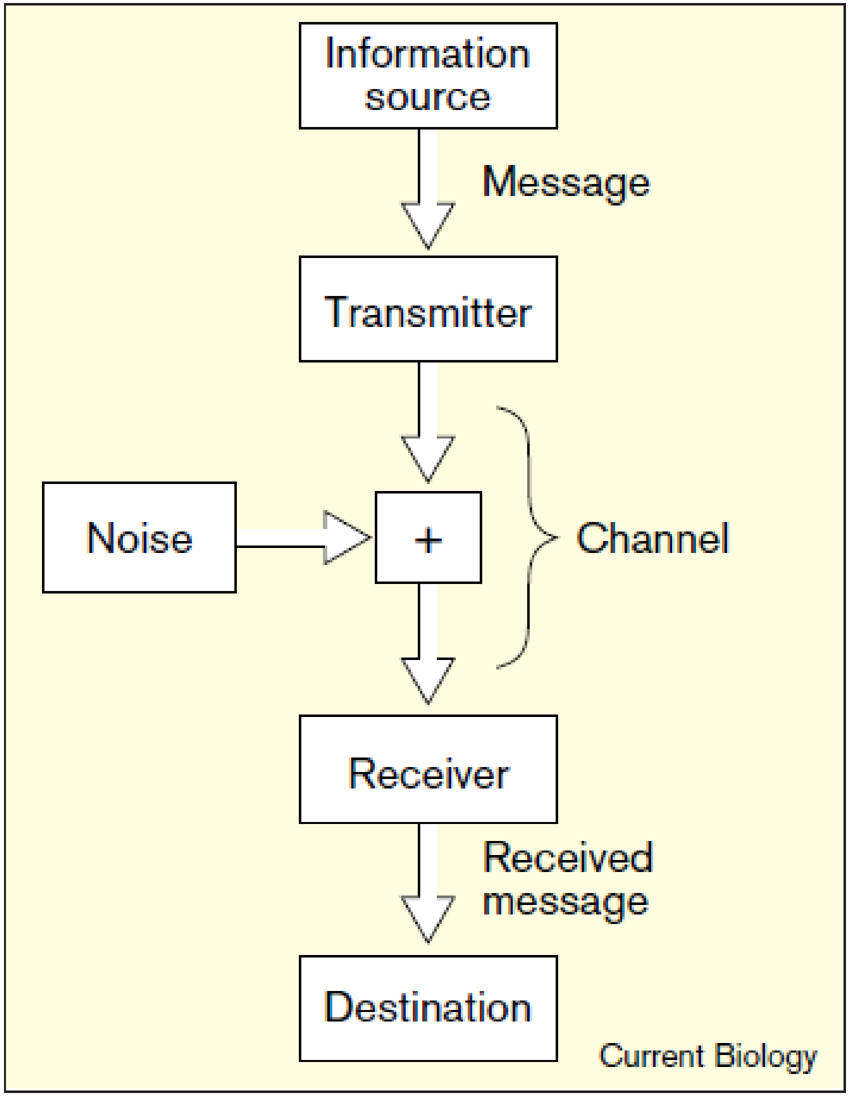
1 bit is needed to report the result of 1 coin toss (2 outcomes)

2 bits are needed to report the result of 2 coin tosses (4 outcomes)

n bits for n tosses (2^n outcomes)

information in bits = $\log_2(2^n) = n$

How we think about information



Stimulus entropy

Response entropy

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Stimulus entropy

This is the amount of information <u>available</u> about the stimulus

Stimulus entropy depends on

- the relative likelihood of each possible stimulus state (each “message”)
- …. summed over all stimulus states, weighted by how often they occur

Entropy is maximized if the number of states is as large as possible, and if they are all equally likely.

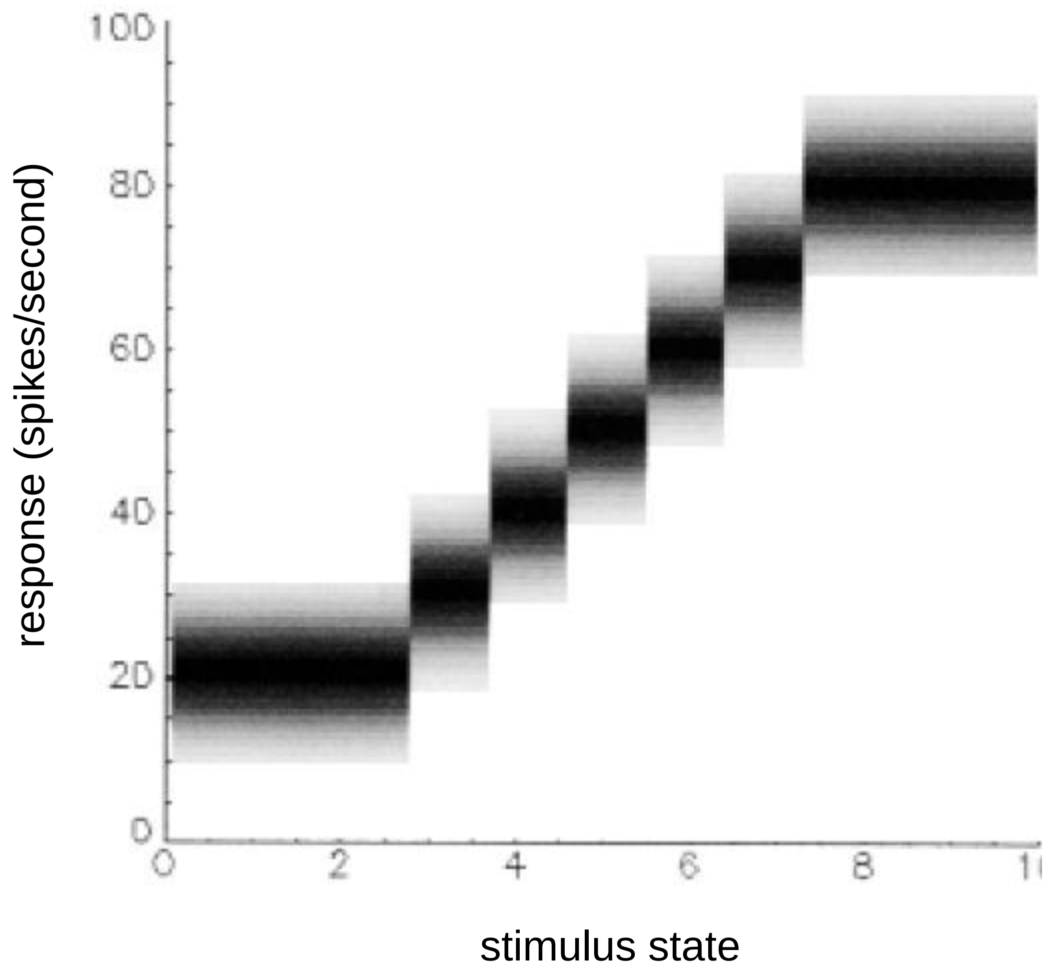
Some messages are more informative than others.

$$\text{Entropy} = \sum P \log_2\left(\frac{1}{P}\right)$$

Response entropy

Neurons have limited dynamic ranges (e.g., no negative or infinite firing rates).

<u>Noise</u> limits the number of discriminable responses within the dynamic range.



Borst & Theunissen 1999 Nature Neuroscience 2:947

Mutual information

Because of noise, not all information from the source is actually received.

Mutual information is defined as the amount by which the received signal actually decreases uncertainty about the source.

Mutual information depends on

- the conditional probability of a stimulus state, given a response value
- … normalized by the individual probabilities of each stimulus state and each response value
- … summed over all stimulus states and response values, weighted according to how often they occur

$$I = \sum_S \sum_R P(S,R) \log_2 \left(\frac{P(S,R)}{P(S) \times P(R)} \right)$$

Mutual information

Response \ Stimulus	Off $p=0.5$	On $p=0.5$
White $p=0.5$	0.25	0.25
Black $p=0.5$	0.25	0.25

mutual information = 0

Response \ Stimulus	Off $p=0.5$	On $p=0.5$
White $p=0.5$	0.5	0.0
Black $p=0.5$	0.0	0.5

mutual information = 1 bit

Reinagel 2000 Current Biology 10:R542

Lessons from information theory

What is the goal of neural processing within a hierarchical circuit?

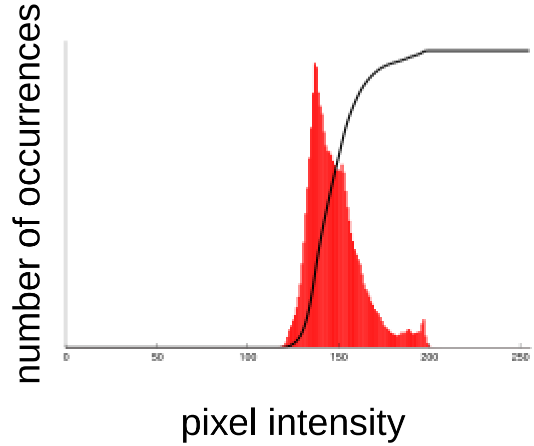
Processing cannot add information!

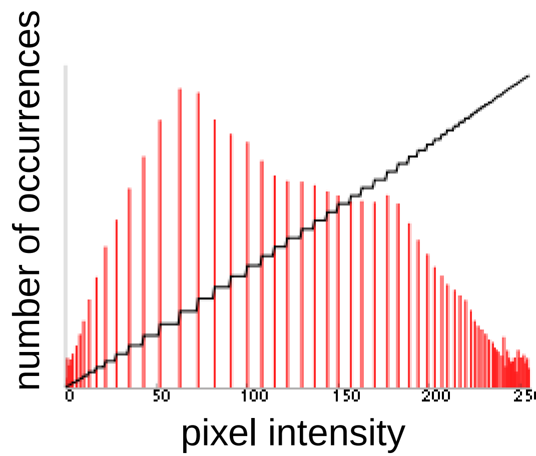
From an information theoretic perspective, processing can only make information more robust to noise contamination.

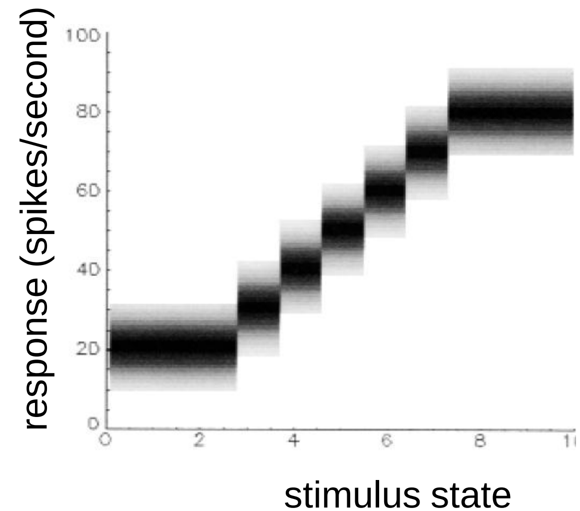
What transformations during processing are potentially useful?

We expect to see some transformations that cause neurons to use their dynamic range more uniformly.

A potentially useful transformation







http://en.wikipedia.org/wiki/Histogram_equalization

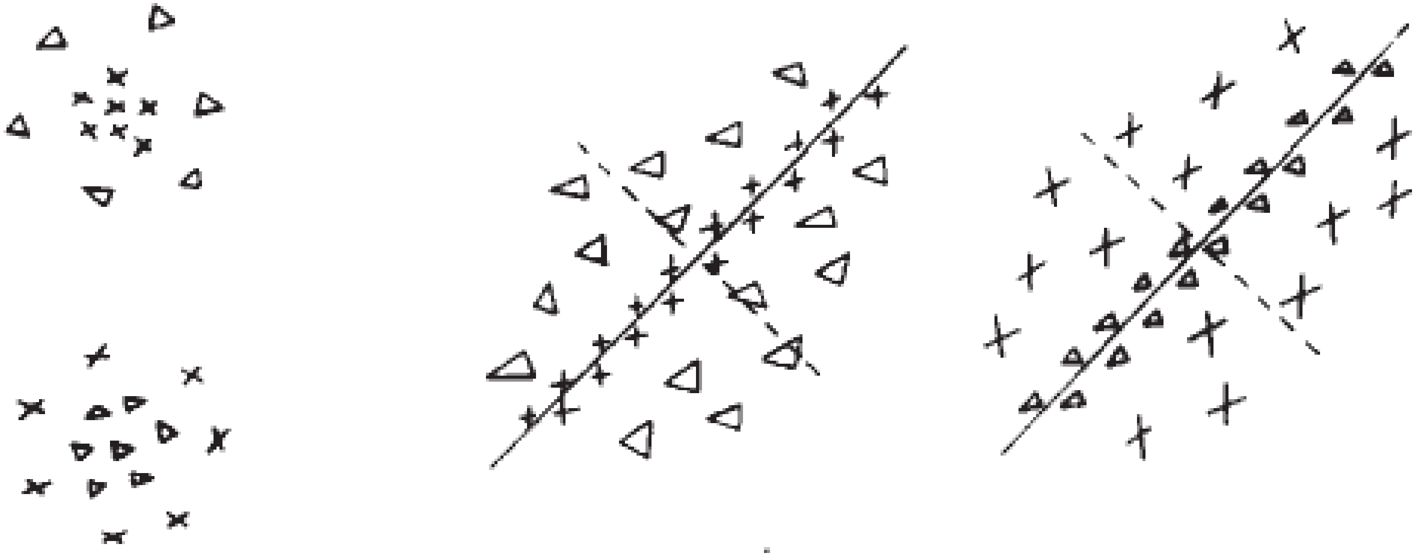
More principles of receptive field structure

- Receptive field structures found in nature are a small subset of all *possible* receptive field structures.
- Receptive fields tend to assign non-zero weights to features that are *adjacent in stimulus space.*
- Receptive fields often contain both positive and negative weights – thereby generating almost no response when adjacent features appear similar.

Natural receptive field structures

visual thalamus and cortex

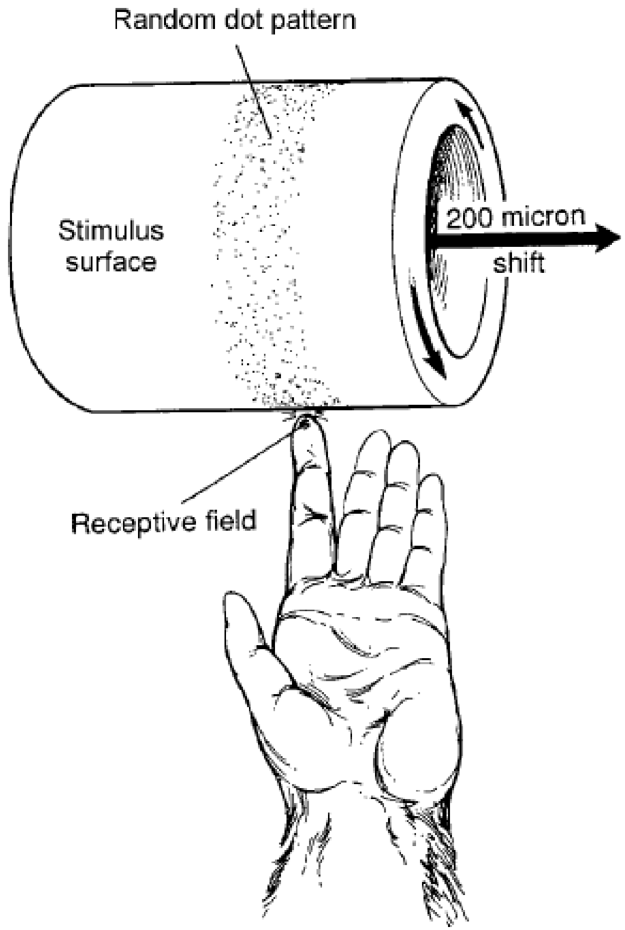
LGN V1



Hubel 1982 Nature 299:515

Natural receptive field structures

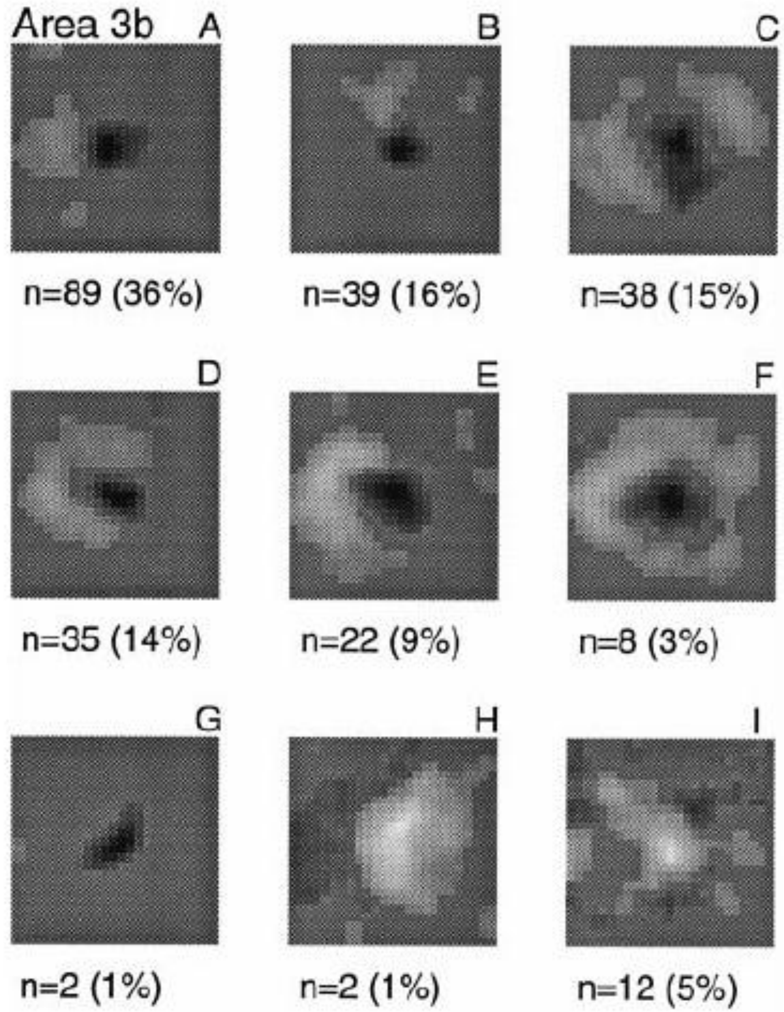
somatosensory cortex



DiCarlo, Johnson, & Hsiao 1998 J Neurosci 18:2626

Natural receptive field structures

somatosensory cortex



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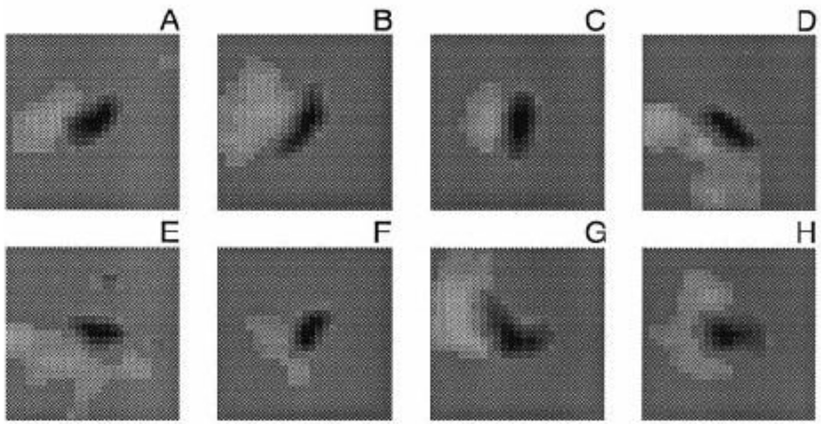
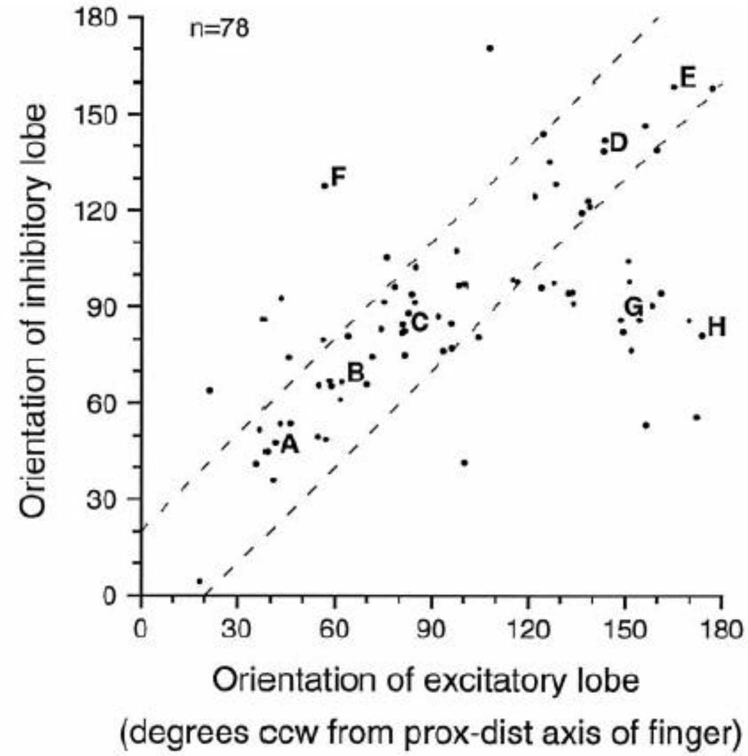
Natural receptive field structures

somatosensory cortex

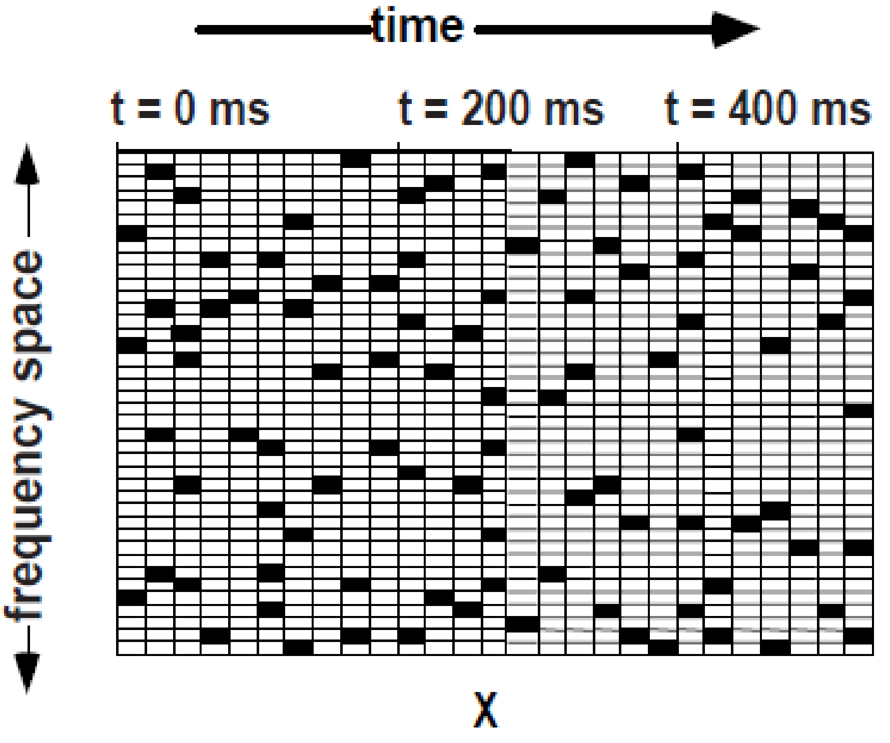




DiCarlo, Johnson, & Hsiao 1998 J Neurosci 18:2626

Natural receptive field structures

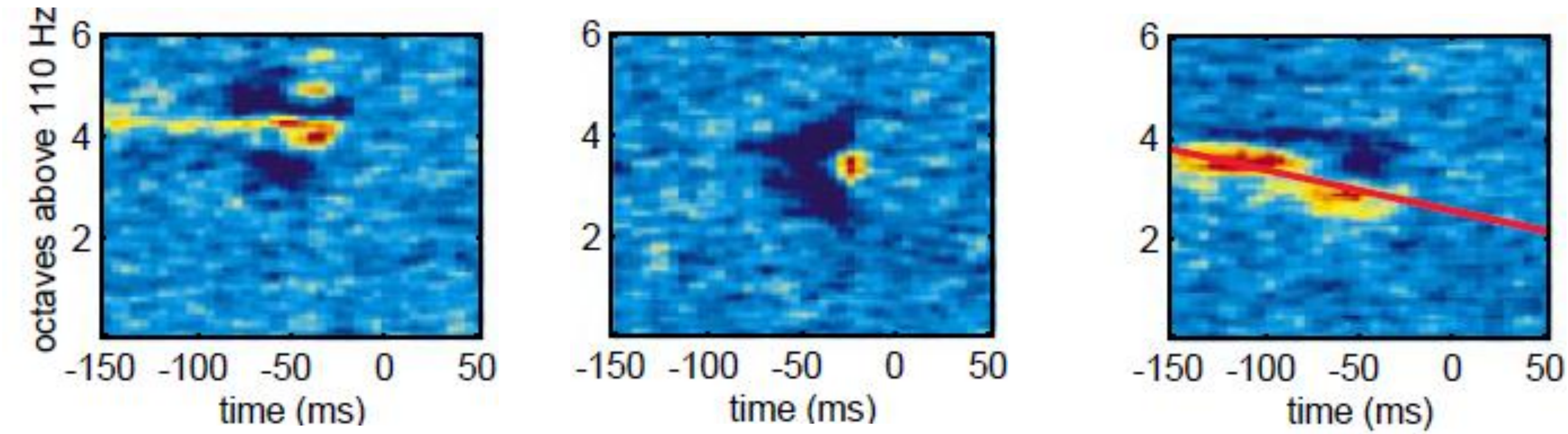
auditory cortex



deCharms & Merzenich 1998 Science 280:1439

Natural receptive field structures

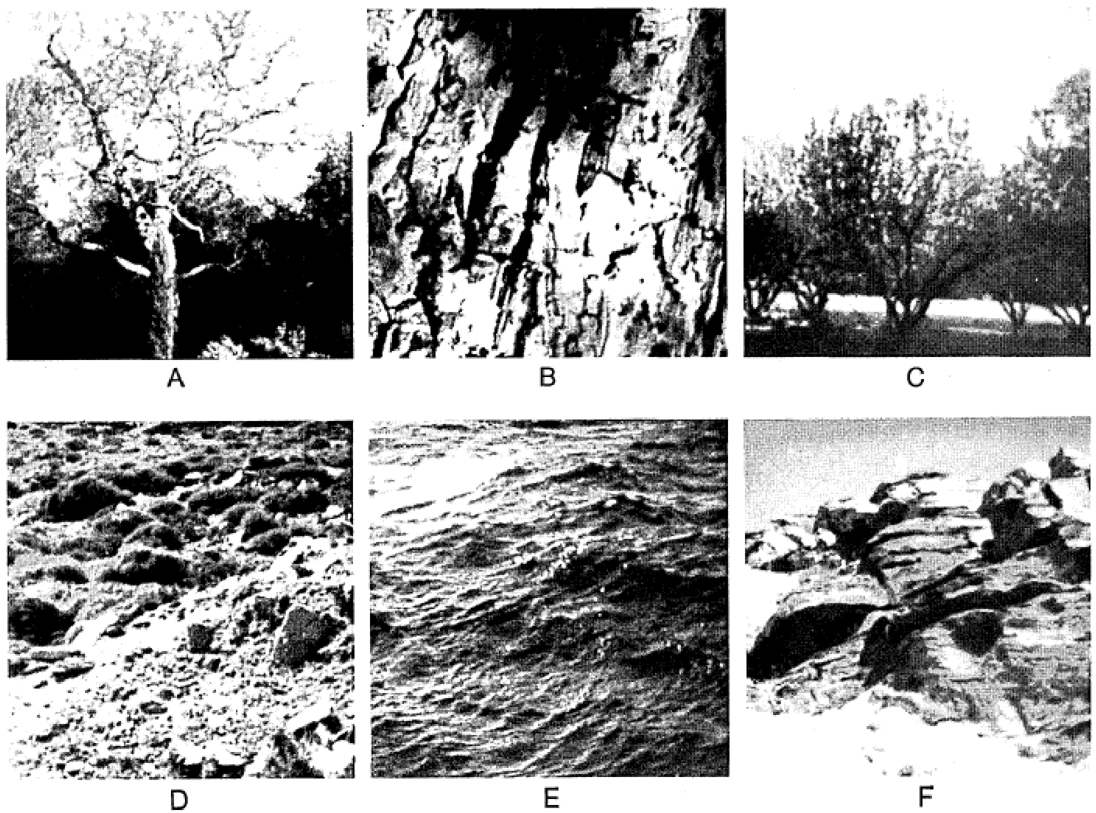
auditory cortex



deCharms & Merzenich 1998 Science 280:1439

Natural statistics

the world has statistical structure

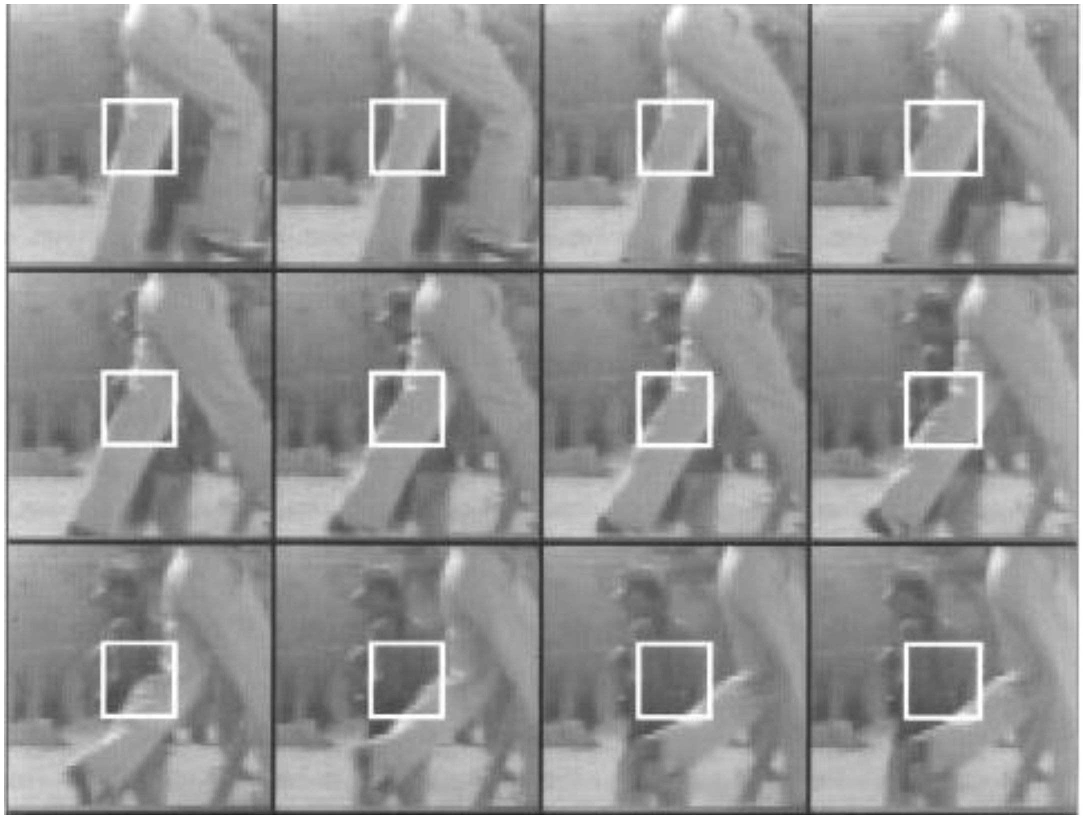


Adjacent spatial features in natural stimuli tend to be similar to each other.

Field 1987 J. Opt. Soc. Am. A 4:2379

Natural statistics

the world has statistical structure



Adjacent temporal features in natural stimuli tend to be similar to each other.

Dan, Atick, Reid 1996 J Neurosci 16:3351

Natural RFs create economical codes

PERCEPTION AS ECONOMICAL DESCRIPTION

FIG. 3. Drawing made by abstracting 38 points of maximum curvature from the contours of a sleeping cat, and connecting these points appropriately with a straightedge.

Attneave 1954 Psychological Review 61:183

Natural statistics and RF structure

Natural RFs can be viewed as creating selectivity for *edges* in stimulus space.

An edge here refers to any sudden discontinuity in stimulus space.

Edges are *unexpected* in natural stimuli.

Natural RFs tend to be selective for stimuli that are unexpected in natural statistical distributions.

More principles of receptive field structure

- As we ascend within a processing hierarchy, we tend to see RFs that are selective for increasingly *behaviorally relevant* stimulus features.

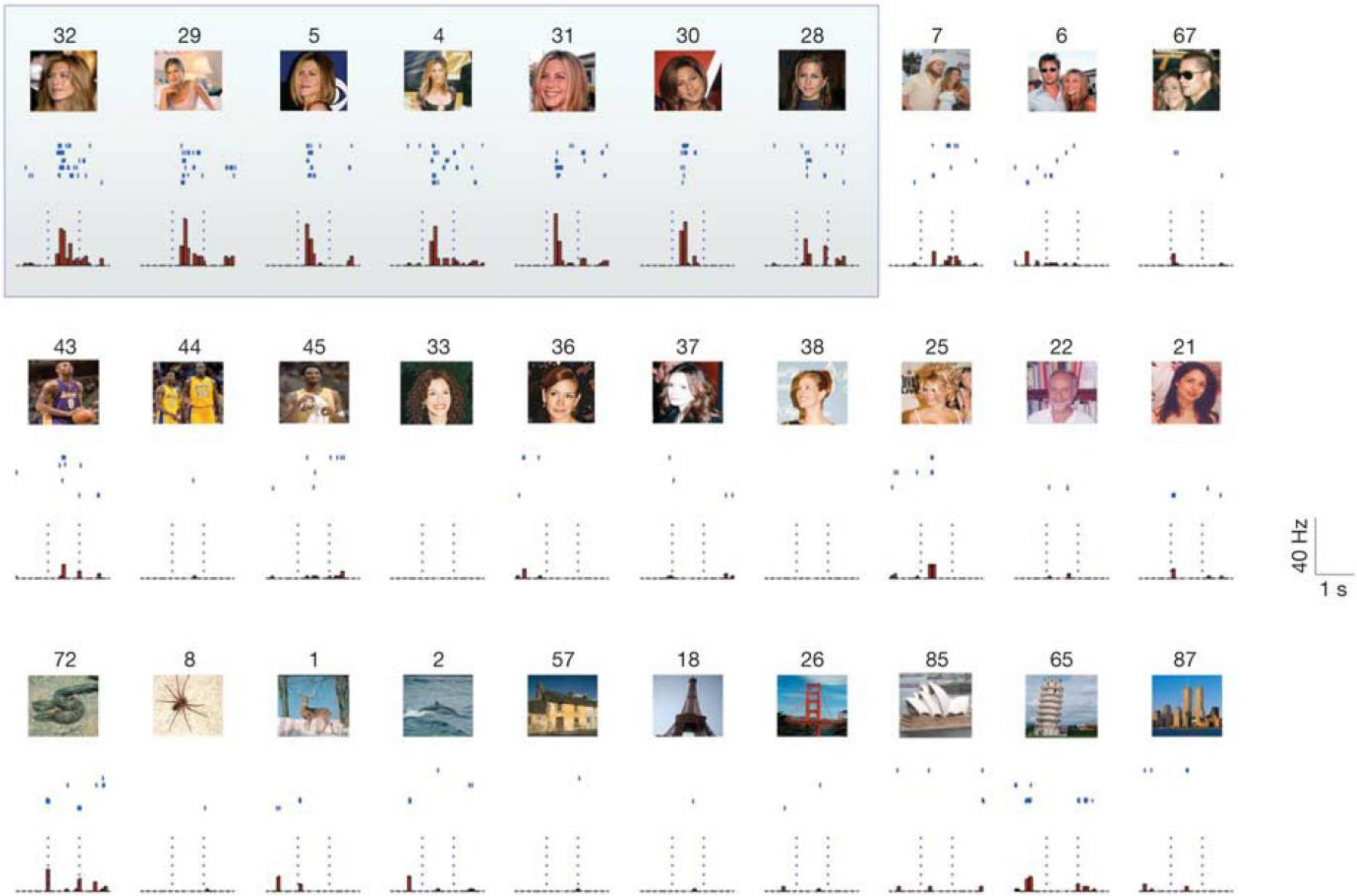
- We also tend to see RFs that are increasingly *invariant* (or at least *tolerant*) to less behaviorally relevant stimulus features.

Selectivity and tolerance

human temporal cortex

Quiroga et al. Nature 2005 435:1102

Selectivity and tolerance



These neurons *tolerant* to face size, retinotopic position, viewing angle, luminance, contrast, clutter, etc.

Quiroga et al. Nature 2005 435:1102

Selectivity and tolerance

[example: semantic content is mainly invariant to pitch]

[example: semantic content depends mainly on temporal modulations]

There must be higher-order auditory neurons in humans that are *selective* for the temporal modulations critical to speech, but also *tolerant* to pitch.

see Quiroga et al. Nature 2005 435:1102

Selectivity and tolerance

A major purpose of neural computations is to make behaviorally relevant stimulus features as <u>explicit</u> as possible (whereas they were only <u>implicit</u> in lower levels).

- face identity is implicit in photoreceptors, explicit in temporal cortex
- semantic content is implicit in cochlear hair cells, explicit in temporal cortex

Selectivity for behaviorally relevant stimulus features <u>necessarily</u> implies invariance or tolerance to less relevant features.

Information and neural computations

Information theory can help us understand the potential utility of some neural computations.

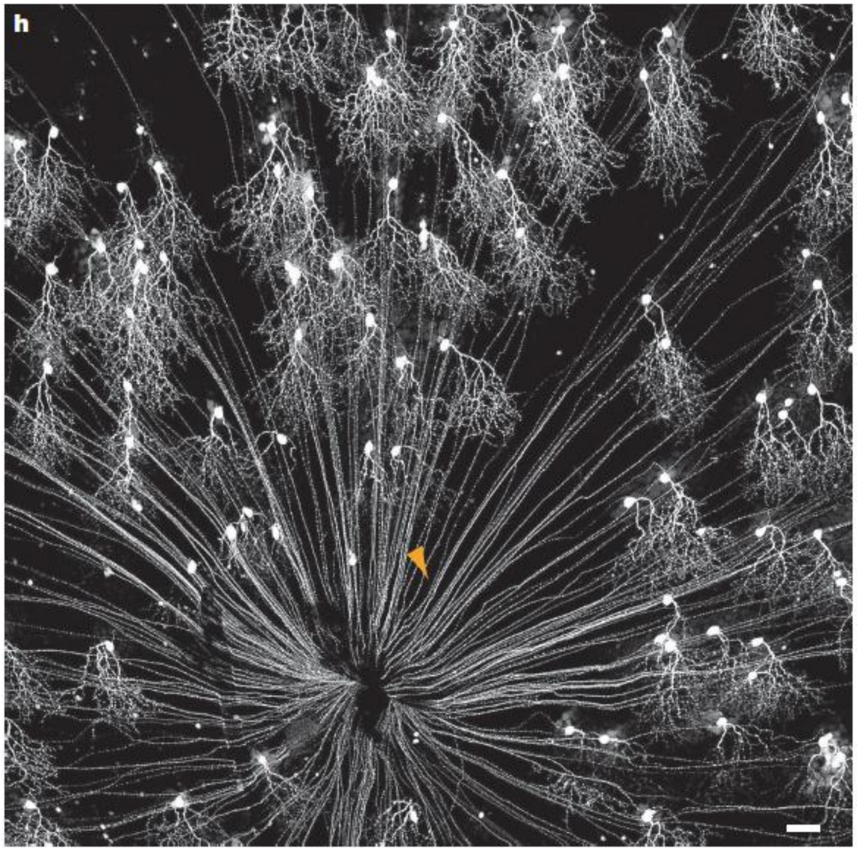
However, information theory is also a fairly impoverished way of viewing neural computations.

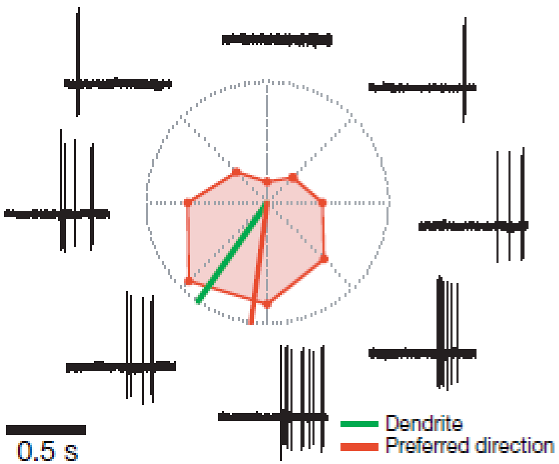
The utility of many computations can only be understood only from the organism's perspective.

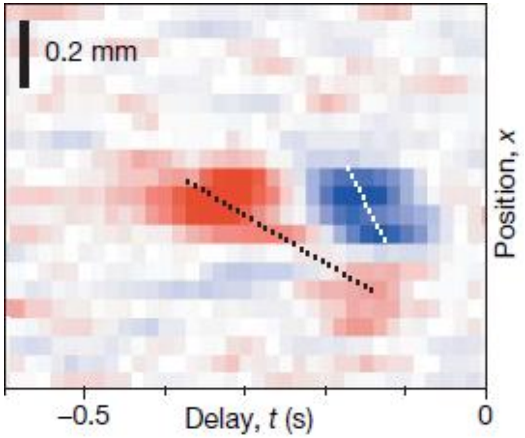
The organism needs to decode information rapidly for the purpose of selecting behavioral actions within the limited repertoire of the organism's ecology.

Seeing from the organism's perspective

JAM-B retinal ganglion cells in mouse







Kim, Zhang, Meister, & Sanes 2008 Nature 452:478