

The Role of Energy Efficiency in Optimizing Biological Information Processing

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Many parametric observations in Nature can be made sensible when interpreted from the perspective of energy efficiency. Some of us have incorporated this energy-efficient perspective into an information-theoretic perspective of brain function. Specifically, neuronal coding and neuronal computation, interpreted from the perspective of energy efficiency, makes sense of the low firing rates and of the high synaptic failure rates observed in forebrain cortical systems.

3

2

4 published results

1. $p^* \Leftrightarrow r$

2. $p^* \Leftrightarrow f$

3. A comparison of p^* for codes:
 $\{0,1\}$
interpulse interval
frequency

4. Velocity costs energy

Energy efficient neural codes.

Levy W. B & Baxter, R. A. 1996

Neural Computation 8:531-543

Energy-efficient neuronal
computation via quantal synaptic
failures.

Levy, W. B & Baxter, R. A . 2002

J. Neuroscience 22:4746-4755

Energy-efficient interspike interval
codes.

Crotty, P. & Levy, W. B 2005

Neurocomputing 65-66:371-378

Conduction velocity costs energy.

Sangrey, T. & Levy, W. B 2005

Neurocomputing 65-66:907-913

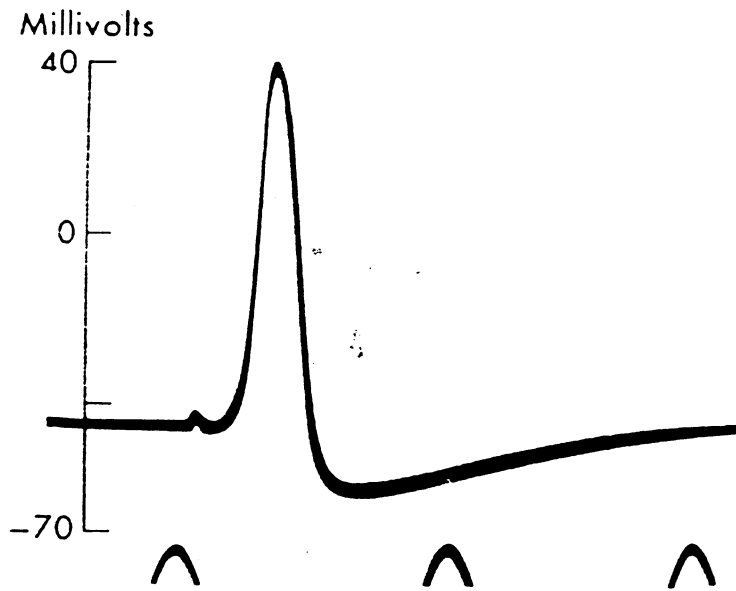
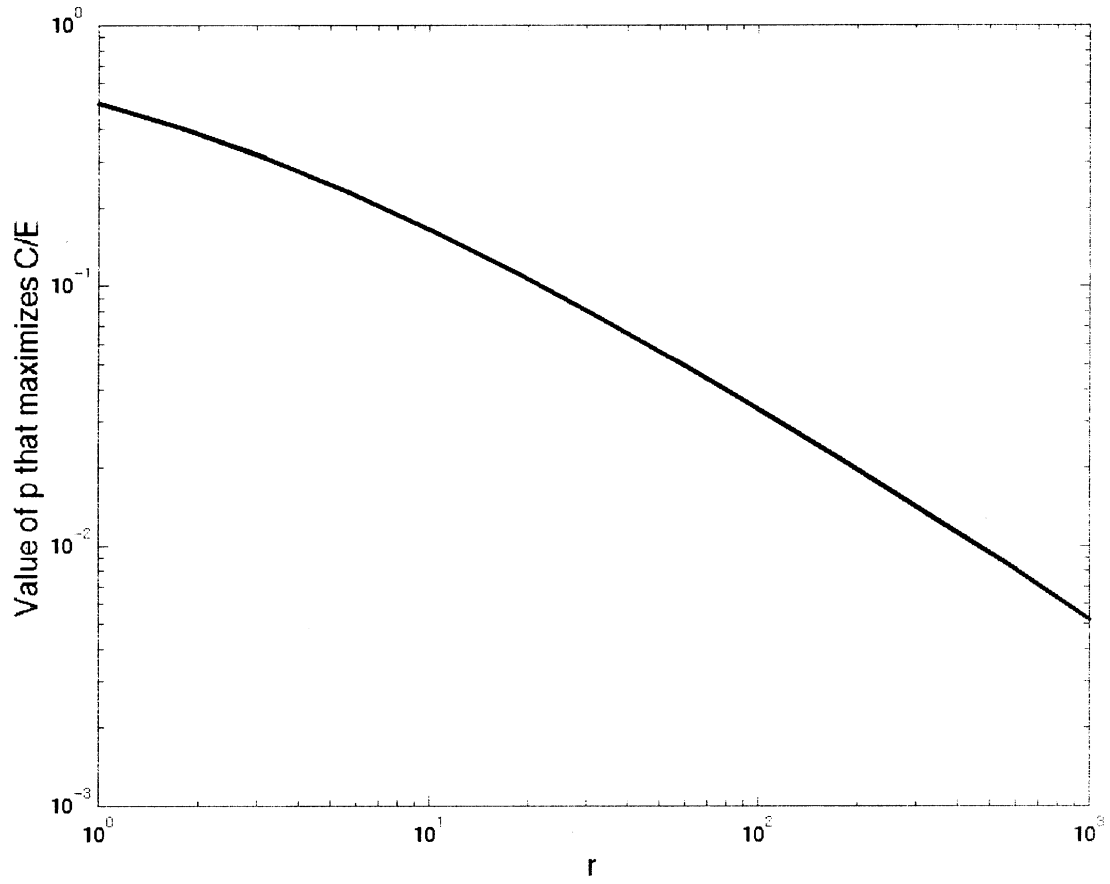
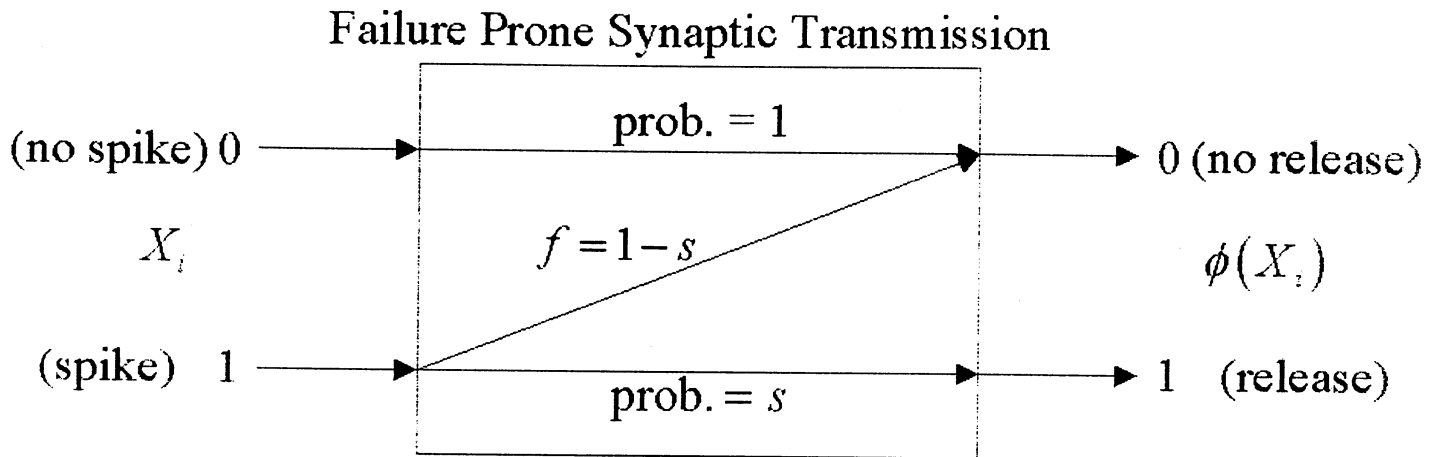


FIG. 2:25. Oscilloscope record for the potential of a capillary electrode inside the squid axon. The initial negative potential at rest is referred to the outside sea water. This potential changes sign during an impulse to overshoot the resting potential. Time, 2 msec intervals.



Synaptic Transmission is Failure Prone



$$f \sim 0.75 !!$$

$$f \approx \left(1/4\right)^{H(p^*)}$$

f – failure rate

p^* – optimal energy-efficient rate
of axonal use

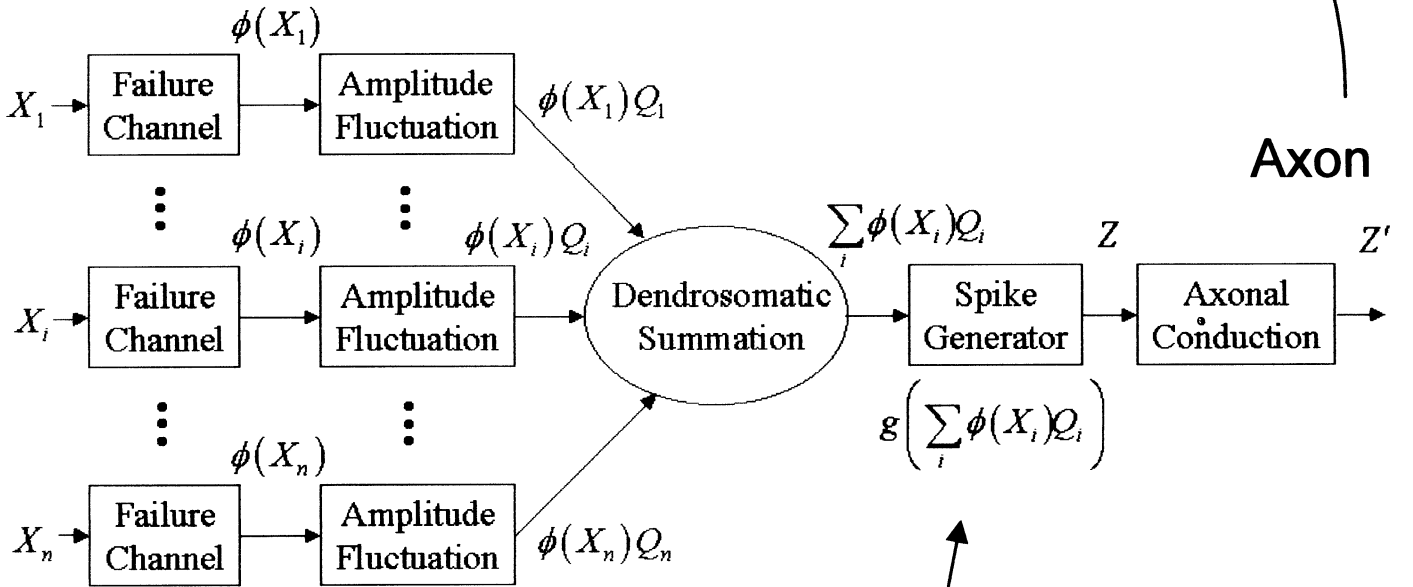
$H(p^*)$ – axonal capacity/mutual
information of axon

Communication

Synapses

Dendrite

Axon



$$I\left(X; \sum_i \phi(X_i)Q_i\right) = H(X) - H\left(X \mid \sum_i \phi(X_i)Q_i\right)$$

$$I(Z; Z') = H(Z) - H(Z \mid Z') \approx H(Z)$$

Analog Computation

Decoding/Encoding

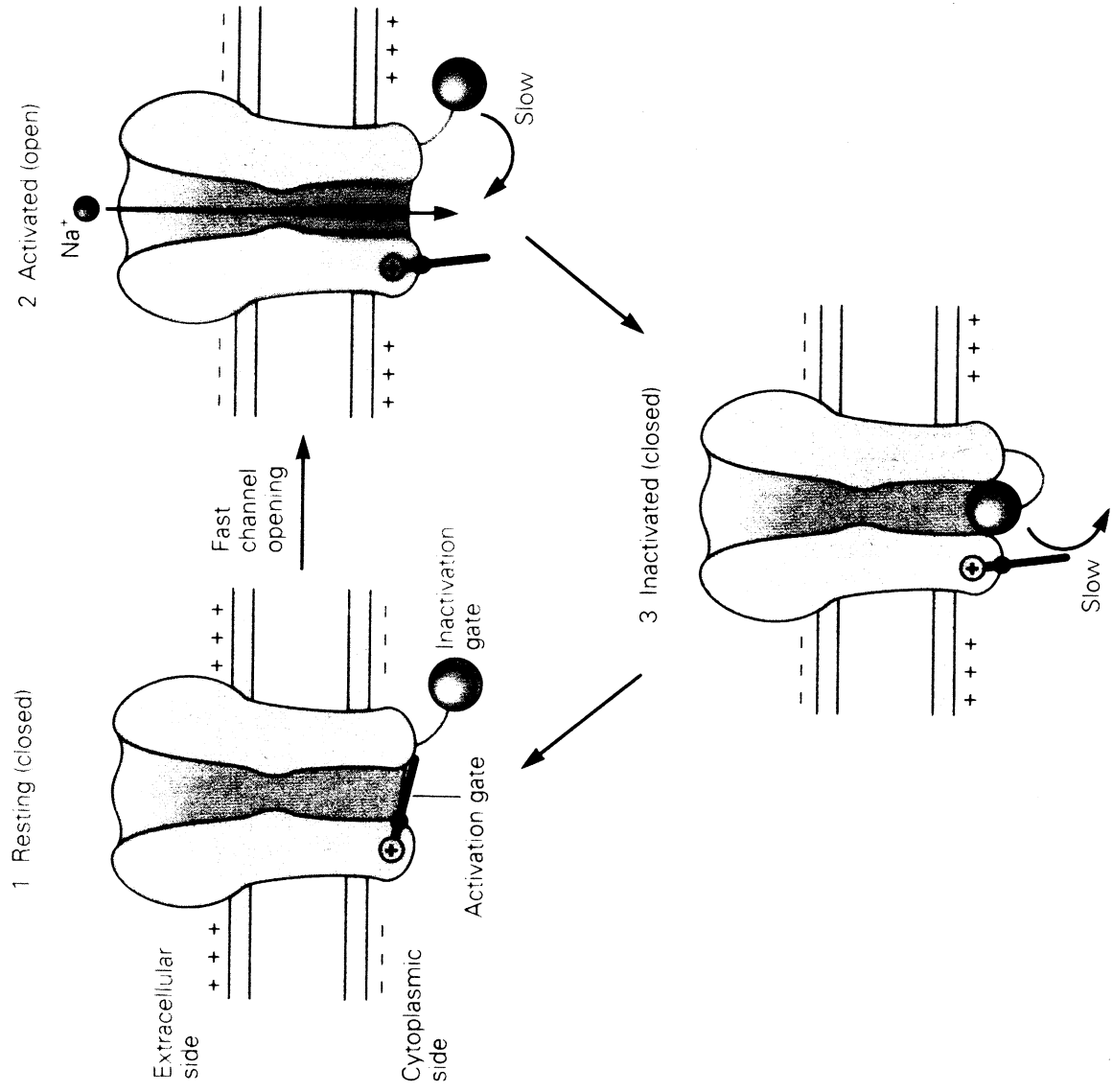
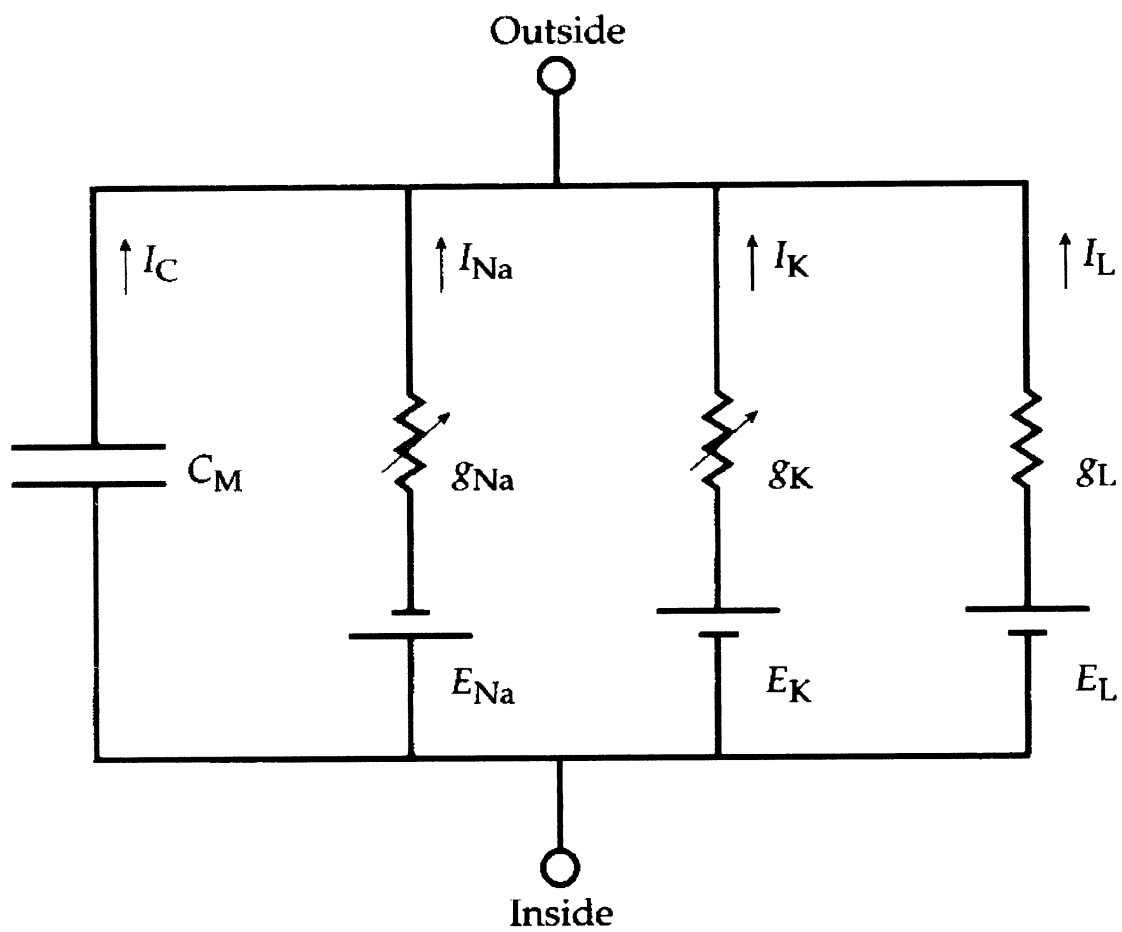


Figure 9-9 Voltage-gated Na⁺ channels have two gates, which respond in opposite ways to depolarization. In the resting (closed) state the activation gate is closed and the inactivation gate is open (1). Upon depolarization a rapid opening of the activation gate allows Na⁺ to flow through the channel (2). As the inactivation gates close, the Na⁺ channels enter the inactivated (closed) state (3). Upon repolarization, first the activation gate closes, then the inactivation gate opens as the channel returns to the resting state (1).



Energy Audit (20-25 watts)

(Attwell & Laughlin 2001)

85-95% of energy goes to
membrane potential (charging
the batteries)

A Nerve Cell has 4 Parts

Axon – long distance electrical
communication, $\{0, 1\}$

Dendrites – analog, electrical computation
[min, max]

Cell body – encoding of analog into
binary

Synapse – very short distance,
chemically-based binary
communication

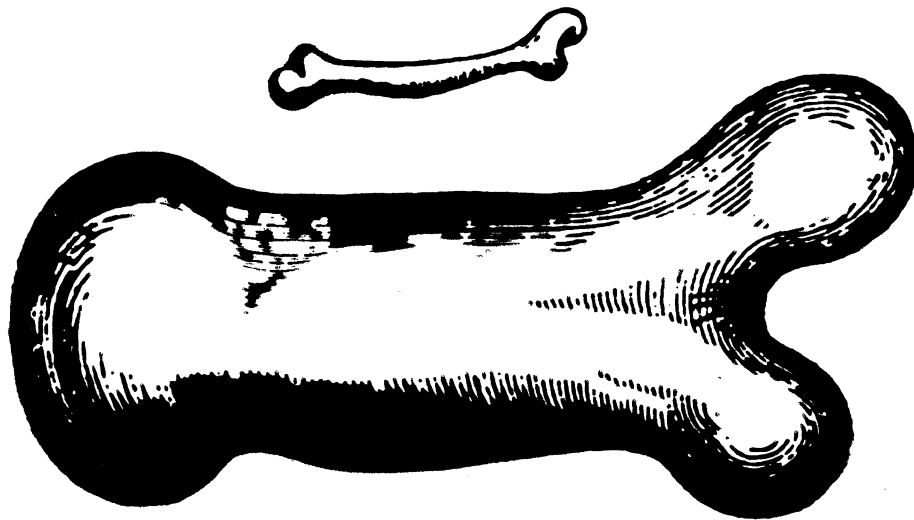
Of this,

58% axons

**35% synaptic activation and
dendrites**

7% transmitter release, etc

An early comment on quantitative constraints



General constraints on computation and communication

- (1) Time
- (2) Space occupied
- (3) Energy
- (4) Information required
- (5) Mass
- (6) Buildability

Why energy efficiency?

Life at the margins is more survivable when energy is of less concern: need less food, less time looking for food; need less oxygen.

Pushing the niche – the margins act as a barrier – too cold/too hot/too deep
too dry/too salty/too not salty enough

Speciation occurs when populations are isolated. Barriers produce isolation. The population living in regions of marginal survival possibilities are functionally isolated.

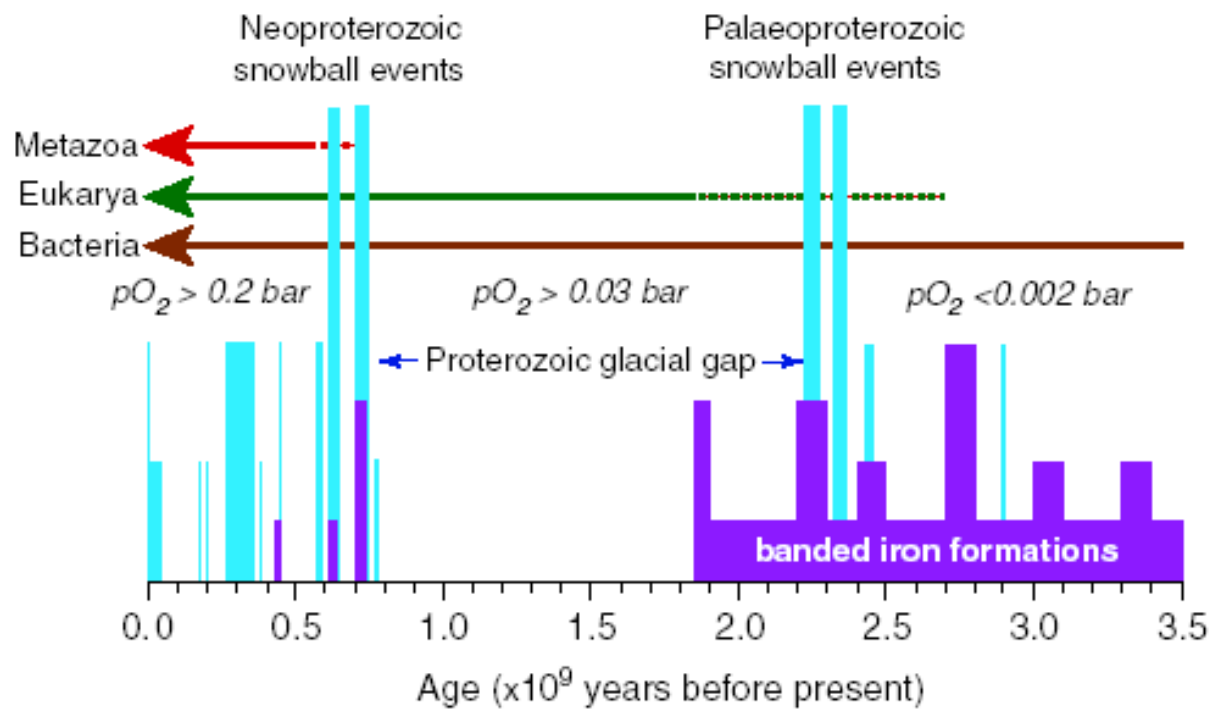


Fig. 12 Frequency of occurrence of iron formations (purple) (modified from Isley and Abbott, 1999), major glacial periods (blue) (Crowell, 1999), constraints on atmospheric oxygen levels (Rye and Holland, 1998), and steps in the history of life. Note the two eras of snowball events separated by a 1.5 billion year gap when evidence is lacking for glaciation at any latitude.

Present atmospheric level of oxygen 20% of atmosphere)

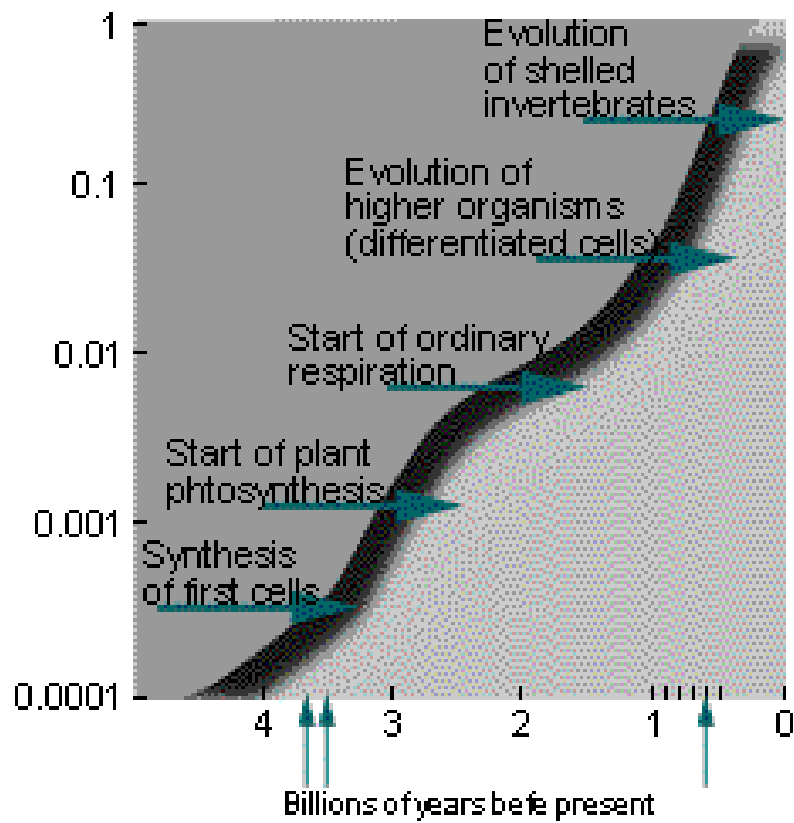
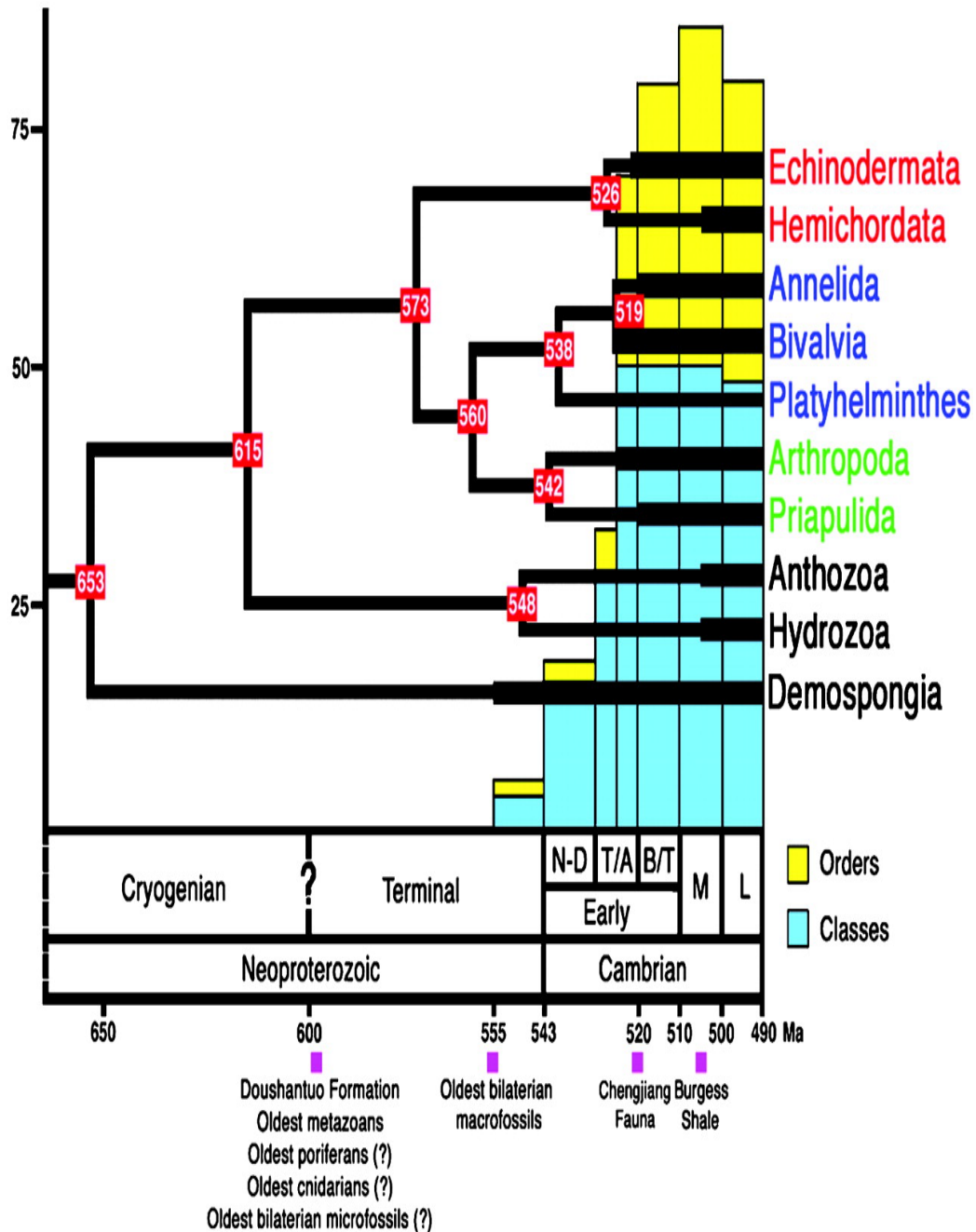


Fig. 4. Metazoan divergence estimates with metazoan diversity and phylogeny placed into the geological context of the Neoproterozoic/Cambrian transition



Peterson, Kevin J. et al. (2004) Proc. Natl. Acad. Sci. USA 101, 6536-6541

Restricted justification of
optimization calculations

Natural Selection is an
optimizing process

But organisms are not
optimal

However, bits and
pieces of
organisms might
be near optimal.

12
1
10
10

Assumption

When a microscopic
feature has remained
unchanged over the eons,
then it must be good at
what it was designed to do.

Example: the
action potential has
not changed for
over 550 million
years.

14
12
11

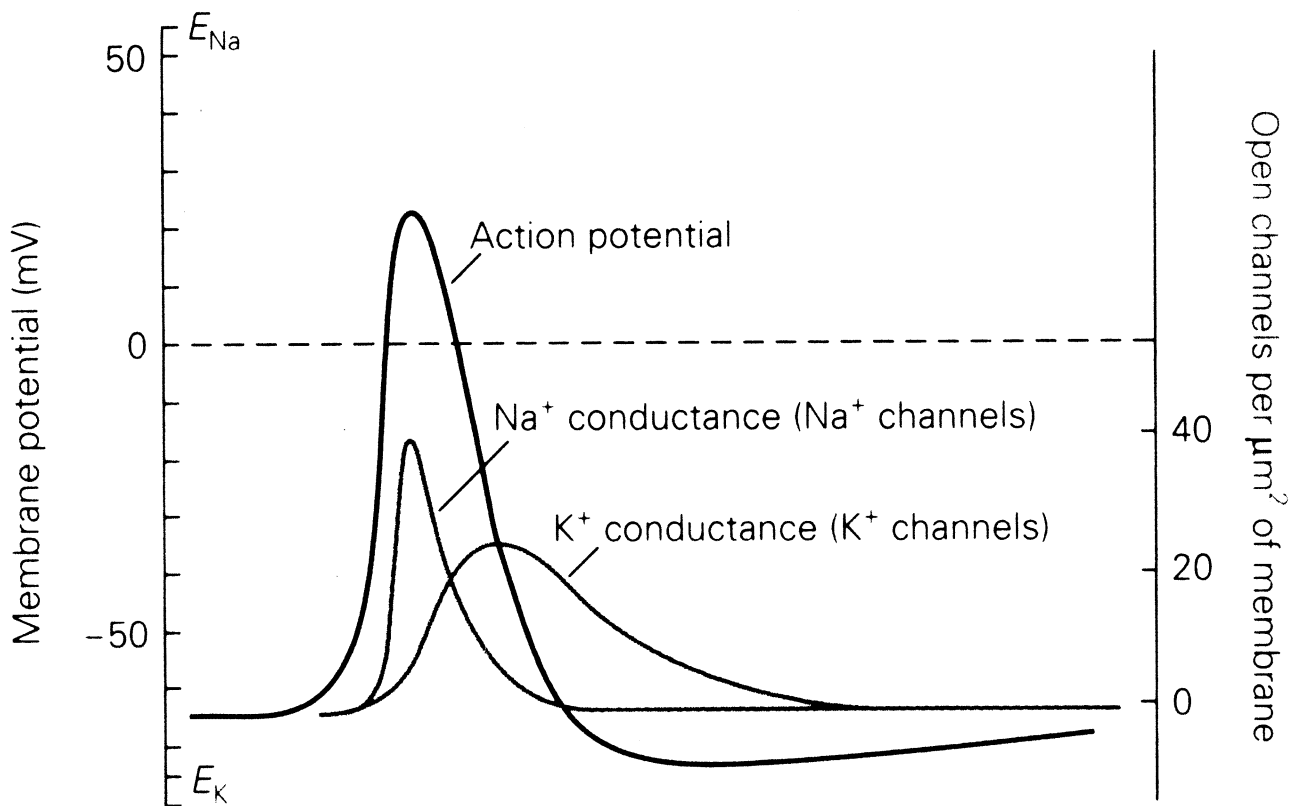
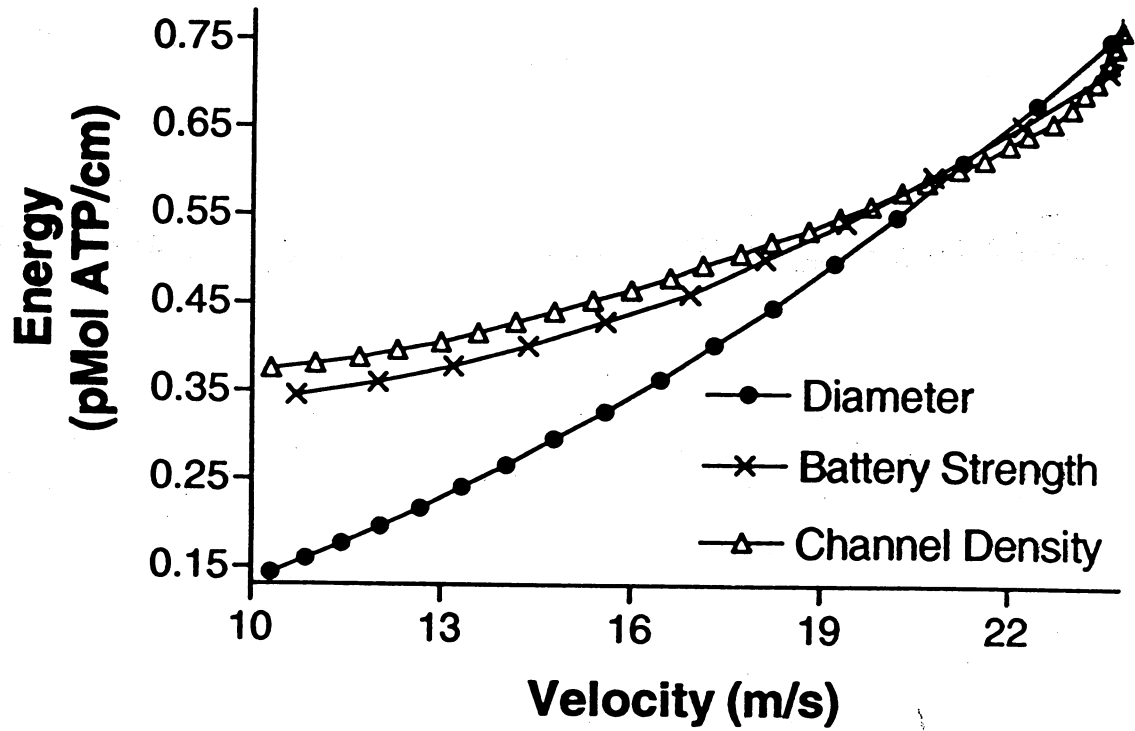
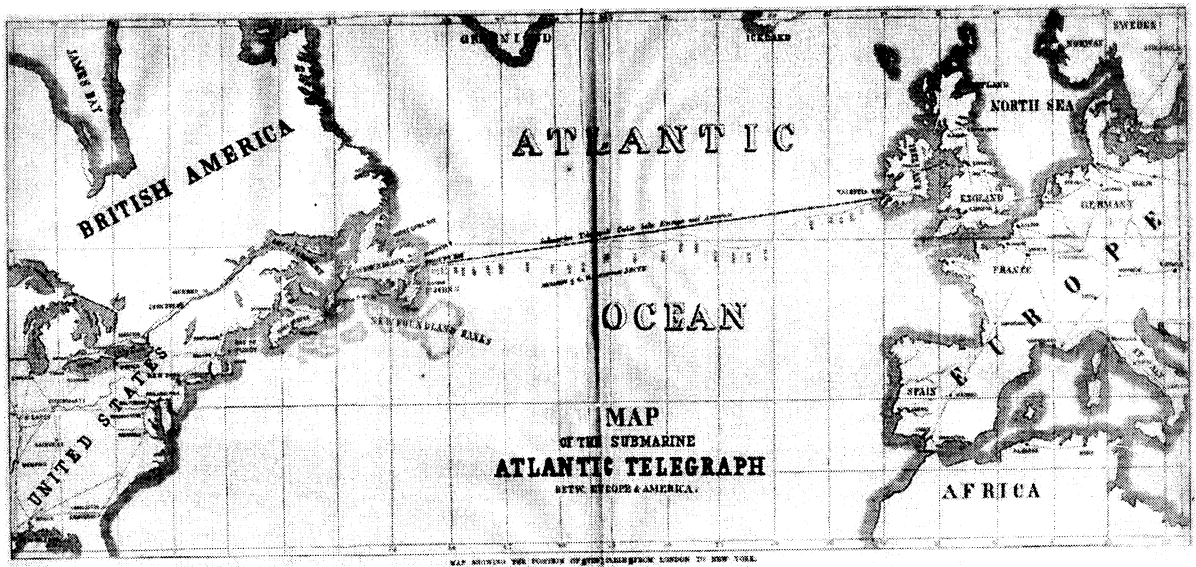


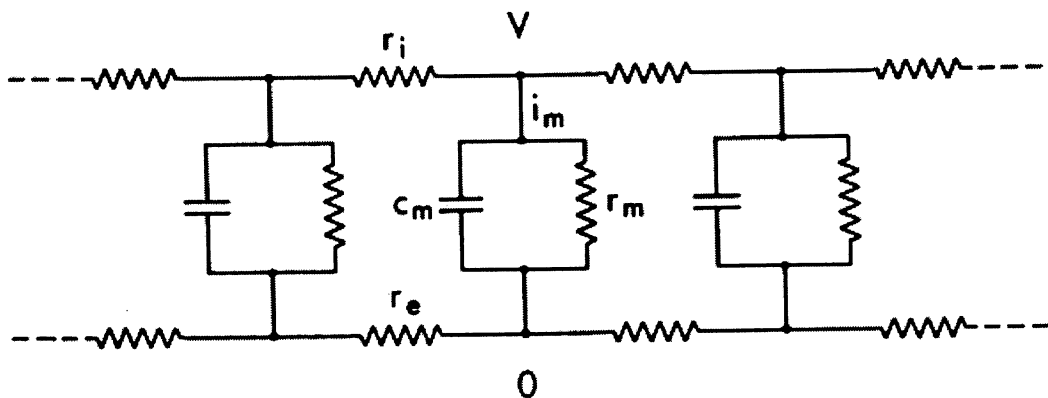
Figure 9-10 The sequential opening of voltage-gated Na^+ and K^+ channels generates the action potential. One of Hodgkin and Huxley's great achievements was to separate the total conductance change during an action potential, first detected by Cole and Curtis (see Figure 9-1) into separate components attributable to the opening of Na^+ and K^+ channels. The shape of the action potential and the underlying conductance changes can be calculated from the properties of the voltage-gated Na^+ and K^+ channels.

Velocity Costs Energy



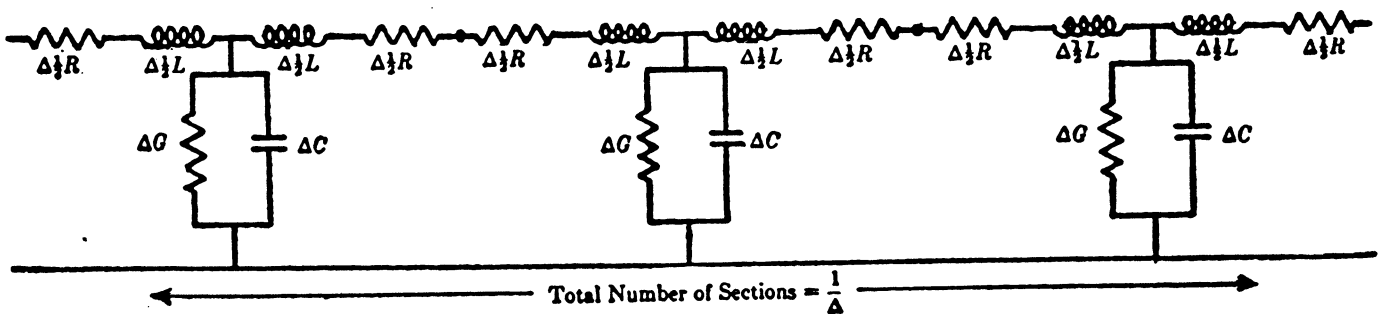


Thompson Transmission Line



$$i_m = c_m \frac{\partial V}{\partial t} + \frac{V}{r_m} = \frac{1}{r_i + r_e} \cdot \frac{\partial^2 V}{\partial x^2}$$

Heaviside Transmission Line



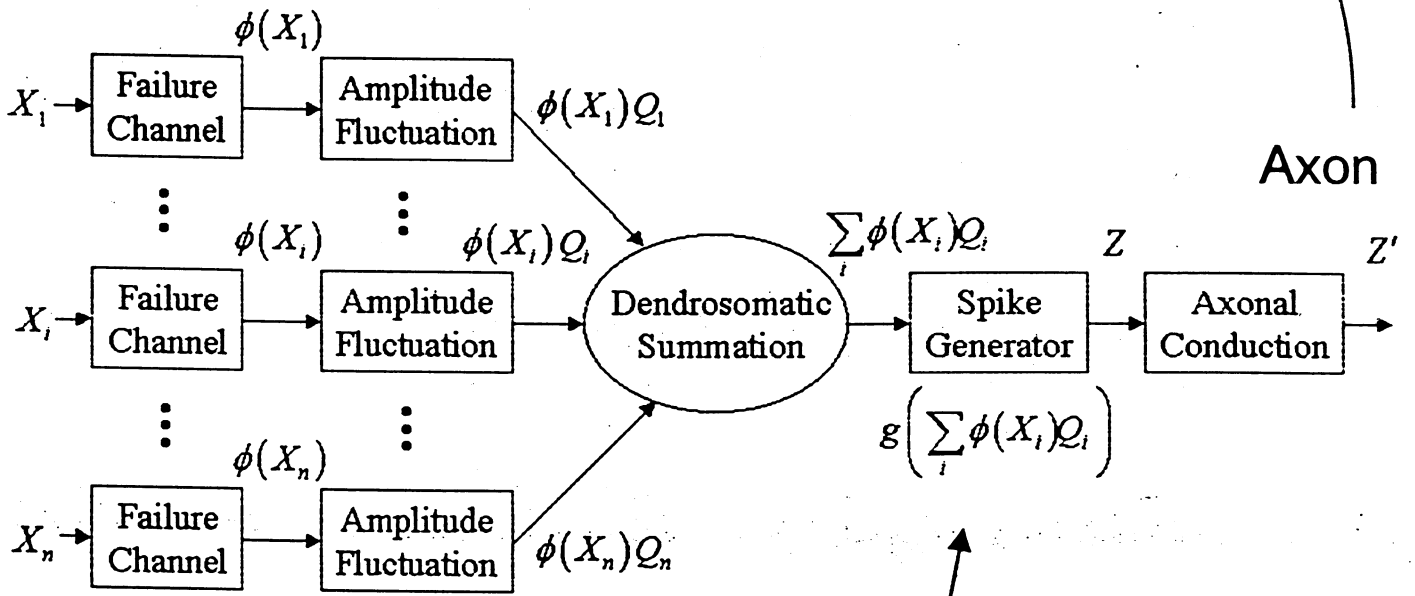
27/

Communication

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Analog Computation

Decoding/Encoding

INFOMAX

Max Mutual Information

$$I(X; Y)$$

Min Statistical Dependency

$$E \left[\log \frac{P(X)}{\prod P(X_i)} \right]$$

$$X \in \{0, 1\}^n$$

Two Problems

1) NOT FULLY CONSTRAINED

How much mutual inf. equals how little stat. dep.?

2) Firing Frequencies are way, way far away from reality

200 Hz vs.

10 Hz

3) Sparse coding/economy of impulses

– unconstrained

Fundamental Insight:

1) Nature has other problems

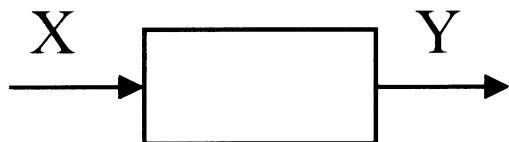
e.g., Energy use

2) ZEROS COST

$I(X;Y)/\text{cm}$ (noise builds up
over distance)

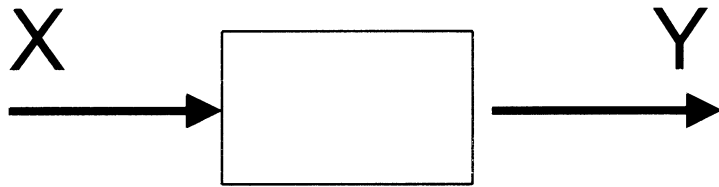
$\text{Ave}(\text{energy})/\text{cm}\cdot\text{s}$

$$\frac{\text{bits}/\text{s}\cdot\text{cm}}{\text{joules}/\text{s}\cdot\text{cm}} = \frac{\text{bits}}{\text{joule}}$$



Infomax

(Barlow, 1959; Linsker, 1989)



$$H(X) \approx H(Y)$$

$$\text{Mutual Inf.} \stackrel{\text{def}}{=} \sum_X \sum_Y P(X, Y) \log \frac{P(X, Y)}{P(X) P(Y)}$$

Stat. Dep. $(Y) \ll (X)$

Economy of Impulses

Sparse Coding

$$H(X) - H(X|Y)$$

$$\gg 0$$

$$\frac{\text{bits/minimal interval cm}}{\text{joules/minimal interval cm}} = \frac{\text{bits}}{\text{joules}}$$

$$= \frac{C}{E}$$

$$\max \left[\frac{C}{E} \right] \equiv \max_p \left[\frac{H(p)}{1+p(r-1)} \right]$$

where p is probability of firing in a minimal interval and r is the ratio of energy expended by a spike relative to a nonspike in a minimal interval

Capacity

$$C = H(p)/\text{computational interval}$$

Energy per computational interval

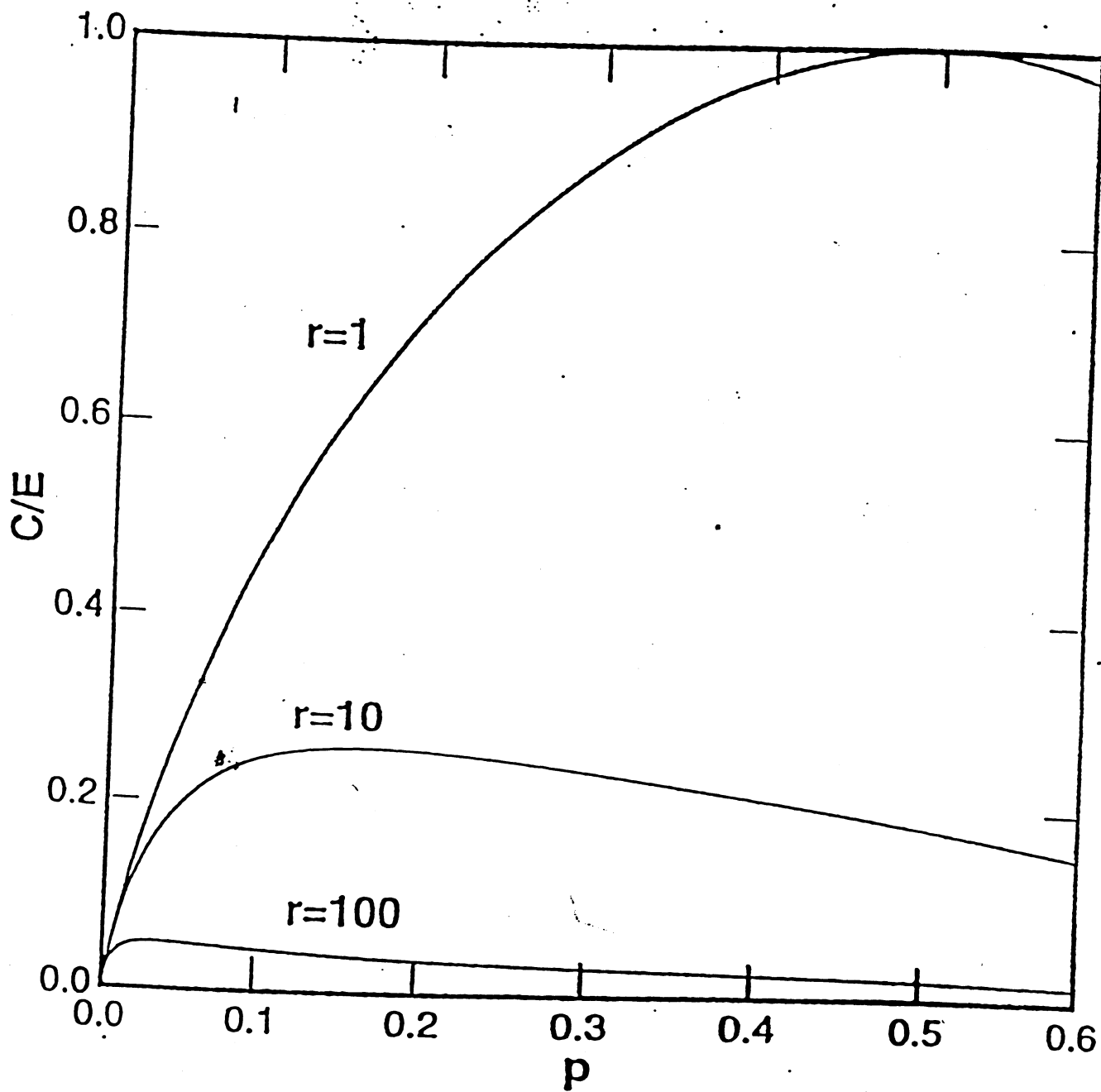
r ratio of cost of action potential vs.
resting for one computational
interval

$$E \propto (1-p) + r \cdot p$$

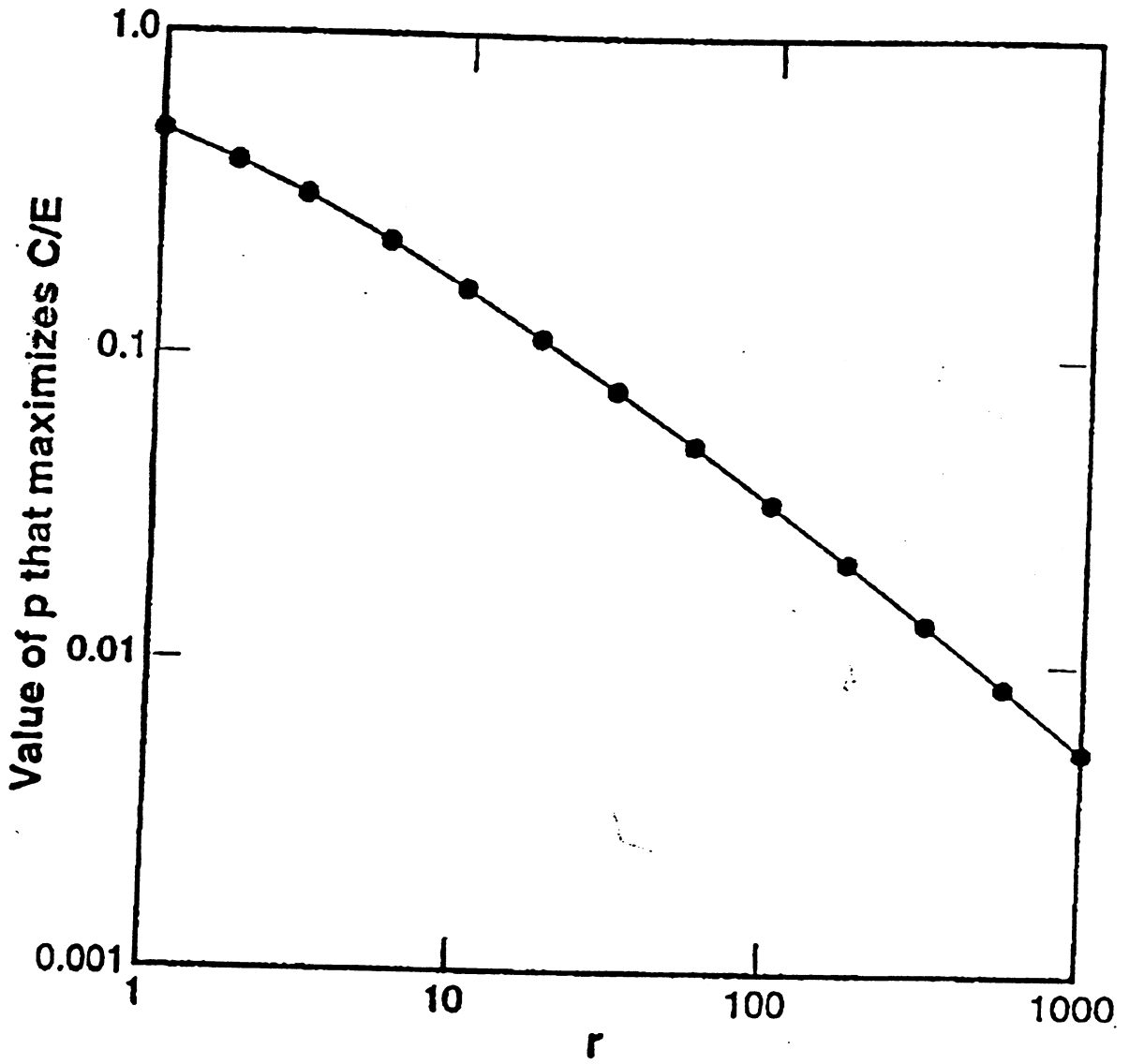
↑
cost of resting in a
computational interval

$$C/E \quad \frac{\text{bits per computational interval}}{\text{energy per computational interval}}$$

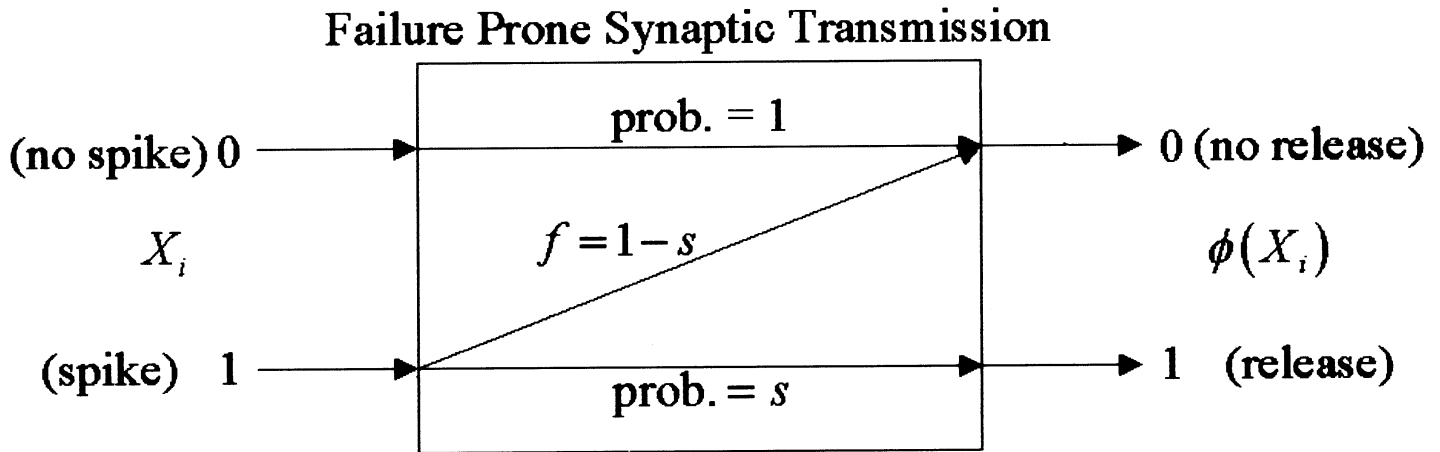
E – ATP, joules, glucose, O₂, etc.



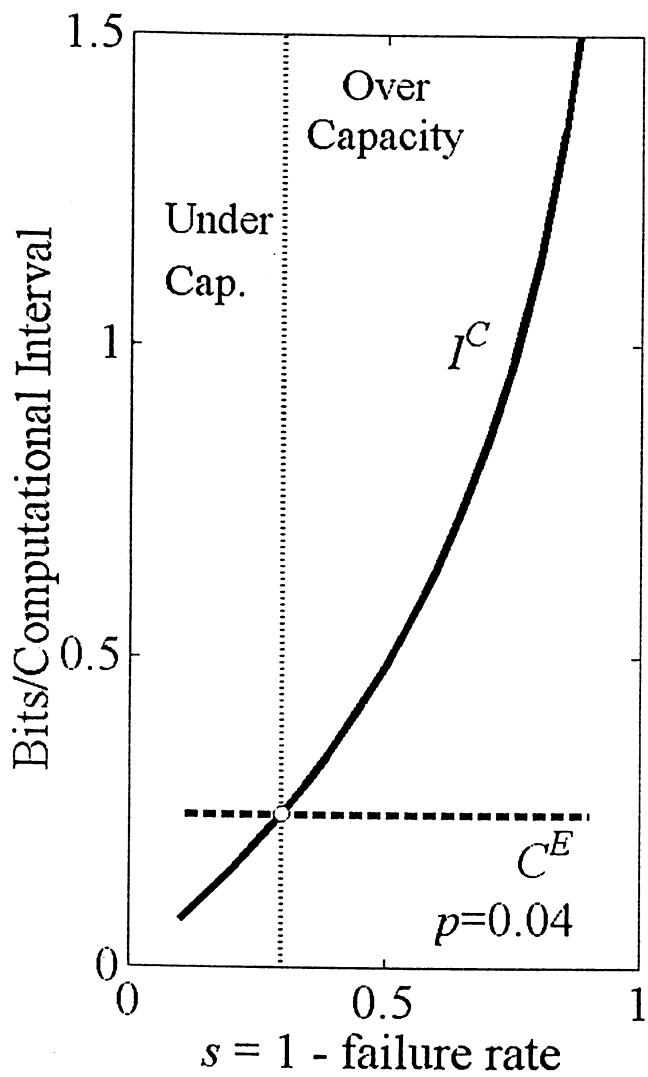
$$\frac{C}{E} \approx \frac{H(p)}{1 + p(r - 1)}$$



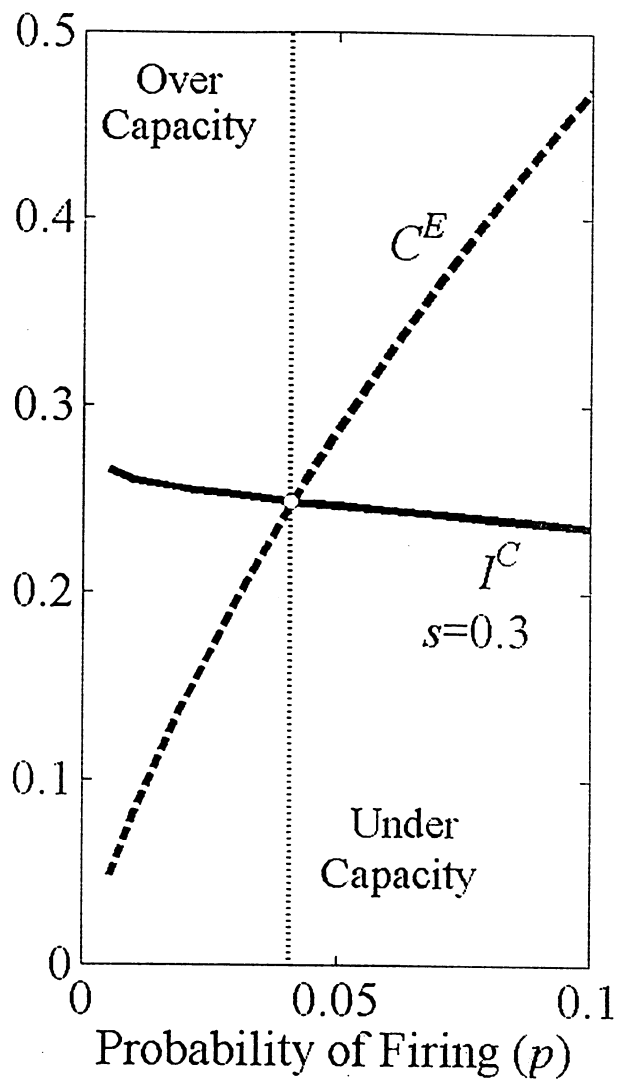
Synaptic Transmission is Failure Prone



$$f \sim 0.75 !!$$



A



B