# Understanding Neuronal Computation and Communication by Analyzing Metabolic Costs

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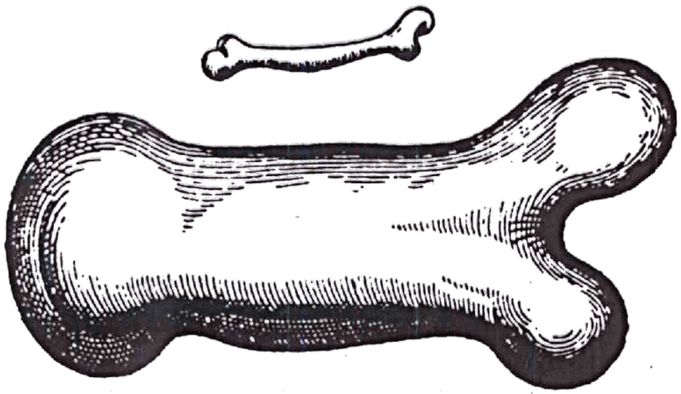
Many parametric observations in Nature can be made sensible when interpreted from the perspective of energy efficiency. Some of us have incorporated this energy-efficient perspective into an information-theoretic perspective of brain function. Specifically, neuronal coding and neuronal computation, interpreted 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.

An early comment on quantitative constraints





General constraints on computation and communication

(1) Time

(2) Space occupied

(3) Energy

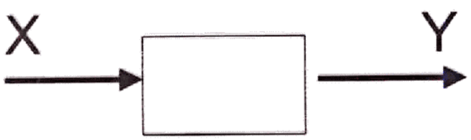
(4) Information required

(5) Mass

(6) Buildability

# Infomax

(Barlow, 1959; Linsker, 1989)




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

Mutual Inf. $\overset{def}{=} \sum_{X}\sum_{Y} P(X,Y) \log \frac{P(X,Y)}{P(X)\,P(Y)}$

Stat. Dep. (Y) << (X)

Economy of Impulses

Sparse Coding



Is there a microscopic constraint that has shaped biological computation?

Hypothesis: microscopically, Neural Communication and Computation are Energy-Efficient

Capacity

C = H(p)/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 $\dfrac{\text{bits per computational interval}}{\text{energy per computational interval}}$

E – ATP, joules, glucose, $O_2$, etc.

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II · 3

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

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

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

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

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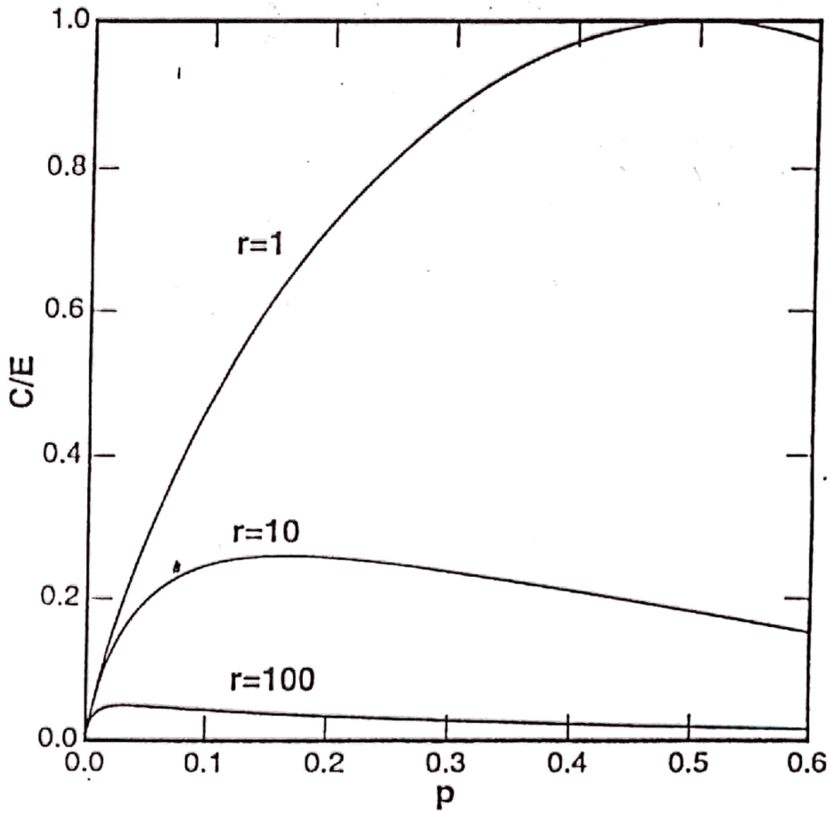
II - 4




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

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II·5

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.

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I·14

Restricted justification of optimization calculations

Natural Selection is an

optimizing process

But organisms are not

optimal

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I-4

However, bits and

pieces of

organisms might

be near optimal.

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I-5

**Assumption**

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

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I-10

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

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I-11

the Heaviside line



such as is shown in Fig. 1. If the total number of sections in such a structure is $1/\Delta$, it is evident that the total series resistance of the

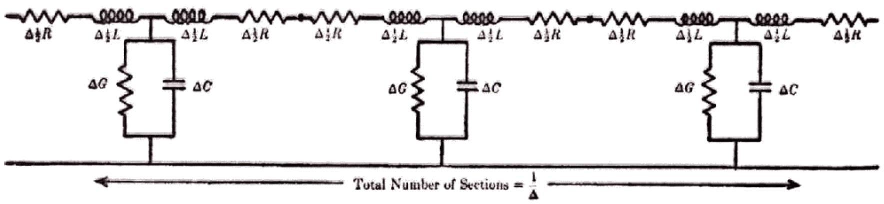


FIG. 1. Recurrent structure having series inductance and resistance, and shunt capacity and leakance.

structure will be $R$ ohms, the total series inductance $L$ henries, the total shunt conductance $G$ mhos and the total shunt capacity $C$ farads.

From equation (1) in Chapter XI, the iterative impedance is

$$Z_K = \sqrt{\frac{\Delta(R + jL\omega)}{\Delta(G + jC\omega)}\left[1 + \frac{1}{4}\Delta(R + jL\omega) \times \Delta(G + jC\omega)\right]} \quad (1)$$

Referring to equation (7) in Chapter XI and the paragraph below it, the total propagation constant, $P$, of the above structure is evidently

$$P = \frac{1}{\Delta} \times 2\sinh^{-1}\frac{1}{2}\sqrt{\Delta(R + jL\omega) \times \Delta(G + jC\omega)} \quad (2)$$

As $\Delta$ approaches zero, the structure (see Fig. 1) evidently approaches that of a line with uniformly distributed constants—the total values of which are $R$, $L$, $G$ and $C$. Under the above assumption regarding $\Delta$, (1) reduces to

$$Z_K = \sqrt{\frac{R + jL\omega}{G + jC\omega}} \quad (3)$$

Also since

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$$P = A + jB = \sqrt{(R + jL\omega)(G + jC\omega)}$$

$L = 0$

$$B = \sqrt{\tfrac{1}{2}\sqrt{R^2G^2 + R^2C^2\omega^2} - \frac{RG}{2}}$$

$$= \sqrt{\tfrac{1}{2}RG}\ \sqrt{\sqrt{1 + \tau^2\omega^2} - 1}$$

$\tau = C/G$ (membrane time constant)

Velocity $= \dfrac{\omega}{B}$ Phase Velocity

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Transmission Circuits For Telephonic Communication, K.S. Johnson, 1927.

$$V = \frac{\omega}{B} = \frac{\omega}{\omega\sqrt{LC}} = \frac{1}{\sqrt{LC}} \qquad (35)$$

This is essentially the velocity of light in the case of a non-loaded circuit. At 800 cycles, the velocity of wave propagation on different types of circuits, as computed by formula (16) and using the circuit constants commercially encountered, is approximately as follows:

| Type of circuit | Velocity-miles per second |
|---|---|
| N.L. No. 12 N.B.S.G. | 174,000 |
| N.L. No. 8 B.W.G. | 178,000 |
| N.L. No. 19 A.W.G. | 39,000 |
| N.L. No. 22 A.W.G. | 28,000 |
| L. No. 12 N.B.S.G. | 56,000 |
| L. No. 8 B.W.G. | 53,000 |
| X.L.L. | 20,000 |
| M.H.L. | 10,000 |

In the above table N.L. designates *non-loaded*, M.H.L. *medium heavy loaded* and X.L.L. *extra light loaded*. The very low speed of wave propagation on loaded circuits is often an objection to their use, especially on long repeatered circuits where *echo effects* and transients may become serious.†

FOR axons
The linear, inductive solution will not work because the very high capacitance leads to a very low velocity (nearly 100 times too slow)



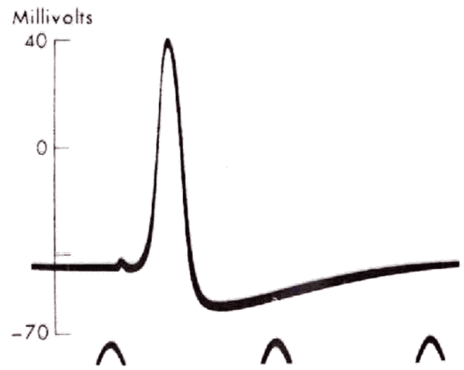
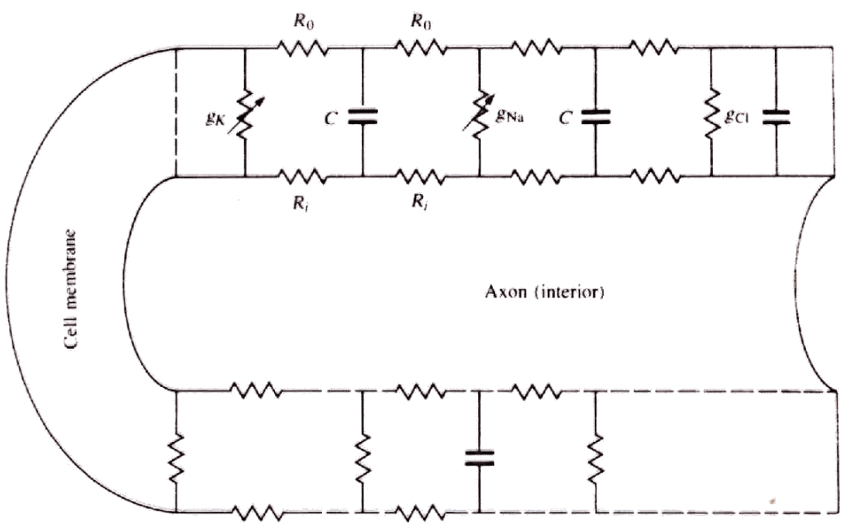



FIG. 2:25. Oscilloscope record for the potential of a capillary electrode inside the squid axon. The initial negative potential at rest is referred to the outside sea water. This potential changes sign during an impulse to overshoot the resting potential. Time, 2 msec intervals.




$$I_{Na} = g_{Na}(\upsilon - \upsilon_{Na})$$
$$I_K = g_K(\upsilon - \upsilon_K)$$
$$I_L = g_L(\upsilon - \upsilon_L)$$

$$\frac{d\upsilon}{dt} = -\frac{1}{C}\left[g_{Na}(\upsilon)(\upsilon - \upsilon_{Na}) + g_K(\upsilon)(\upsilon - \upsilon_K) + g_L(\upsilon - \upsilon_L)\right]$$

$$g_{Na} = \bar{g}_{Na} m^3 h$$
$$g_K = \bar{g}_K n^4$$

$$\frac{dn}{dt} = \alpha_n(\upsilon)(1-n) - \beta_n(\upsilon)n$$
$$\frac{dm}{dt} = \alpha_m(\upsilon)(1-m) - \beta_m(\upsilon)m$$
$$\frac{dh}{dt} = \alpha_h(\upsilon)(1-h) - \beta_h(\upsilon)h$$

$$\alpha_m(\upsilon) = 0.1(v+25)\left(e^{(v+25)/10} - 1\right)^{-1}, \beta_m(\upsilon) = 4e^{\upsilon/18}$$
$$\alpha_h(\upsilon) = 0.07e^{\upsilon/20}, \beta_h(\upsilon) = \left(e^{(v+30)/10} - 1\right)^{-1}$$
$$\alpha_n(\upsilon) = 0.1(v+10)\left(e^{(v+10)/10} - 1\right)^{-1}, \beta_n(\upsilon) = 0.125e^{\upsilon/80}$$

$$\frac{1}{\theta^2 (r_1+r_2)} \frac{d^2 V_m}{dt} = C \frac{dV_m}{dt} + I_g$$

transmemb. ohmic current

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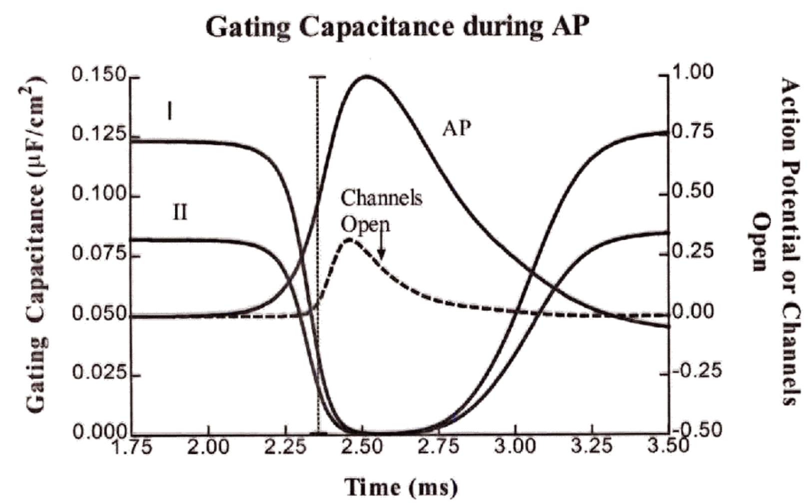
FIG 3

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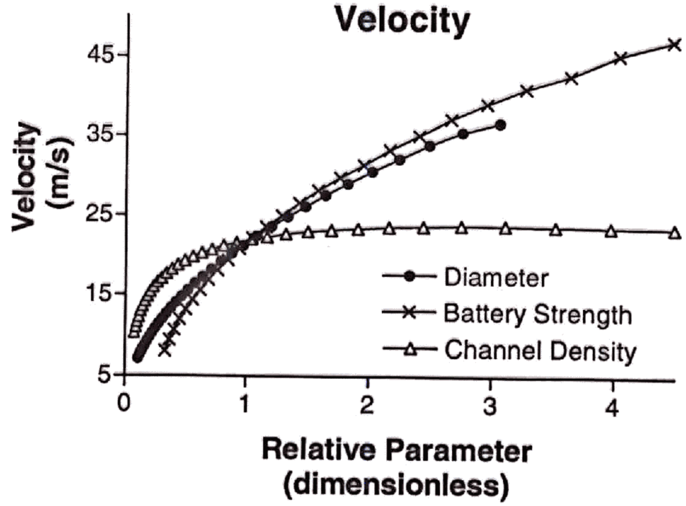
But

**Axon is not Optimized for Velocity**

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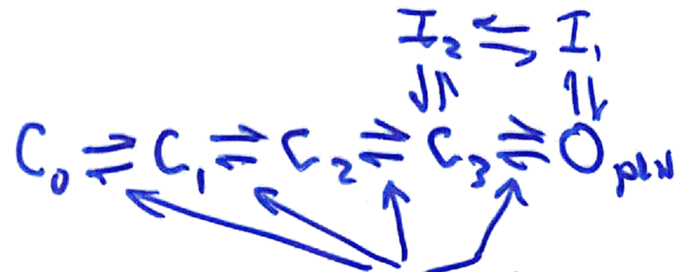
# A Serial Model




gating changes at each stage may total to ~6e

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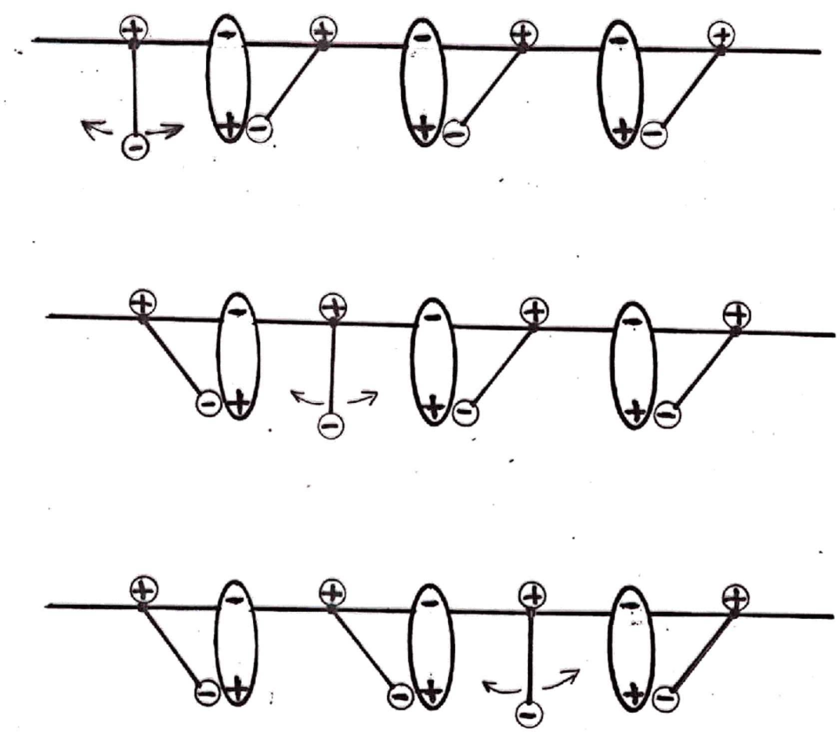

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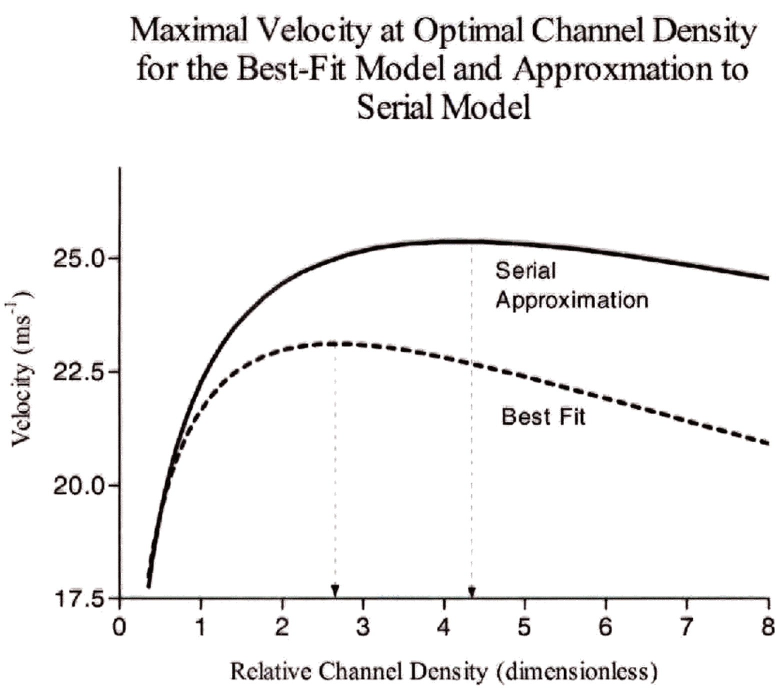
Maximal Velocity at Optimal Channel Density
for the Best-Fit Model and Approxmation to
Serial Model
Velocity (ms⁻¹)
25.0
22.5
20.0
17.5
0
1
2
3
4
5
6
7
8
Relative Channel Density (dimensionless)
Serial
Approximation
Best Fit

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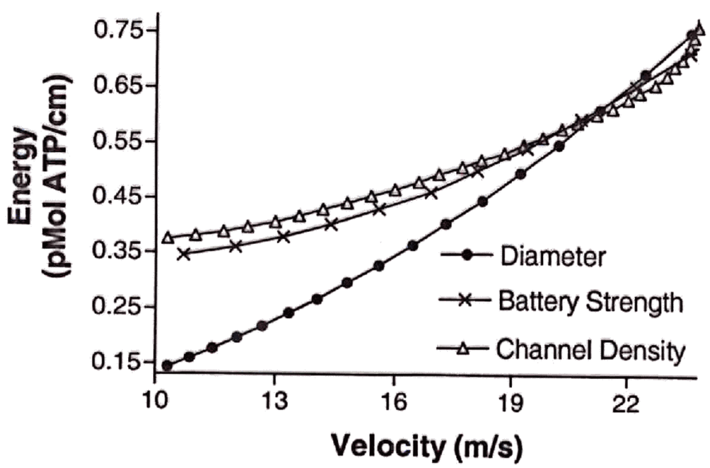
## Velocity Costs Energy

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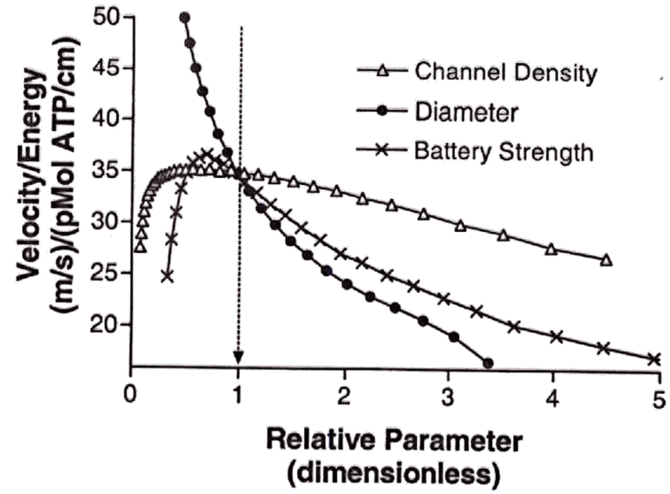
Trying to optimize without regard to temporal delay

## Efficiency for Three Parameters

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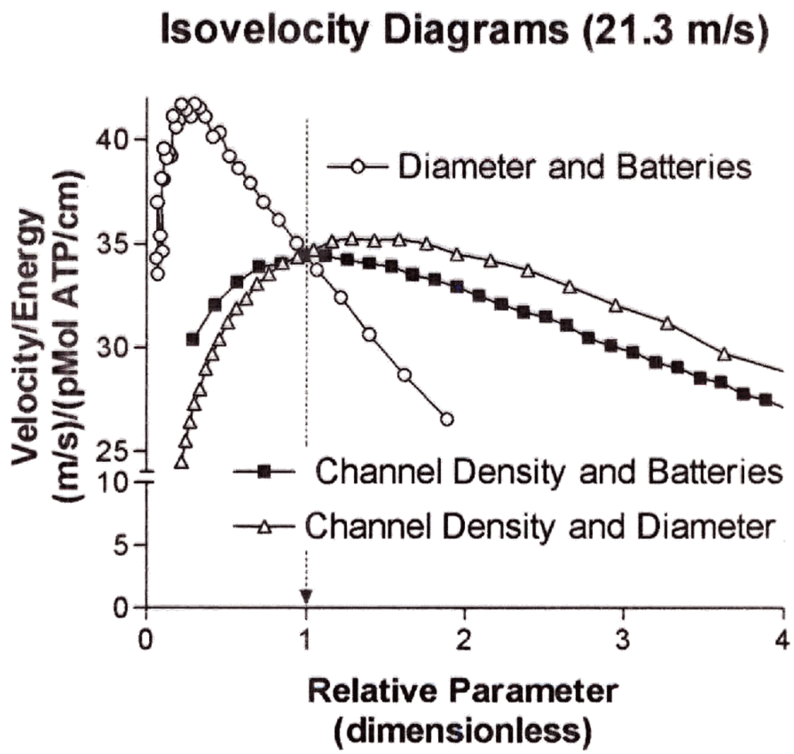
But if timeliness of information matters:




X Axis refers to first parameter of pair.



Conclusions

the energy efficiency of signaling includes information rate and velocity.

1) We conjecture that the action potential is efficient from both perspectives

2) the ultimate limits are set by plasma membrane capacitance and even more basic cell physiology such as the $Na^+$-$K^+$ ATPase that sets the Nernst batteries.