CONSERVED RELATIONSHIPS AND TRADE-OFFS IN THE BRAIN DESIGN

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OUTLINE OF THE TALK:

- INVARIANTS IN THE CORTEX
- MICROSCOPIC VS. MACROSCOPIC CONNECTIVITY
- TRADE-OFFS IN THE CORTEX DESIGN / FUNCTIONALITY

INVARIANTS IN THE CORTEX

- SURFACE DENSITY OF NEURONS

$$\rho = \frac{N}{W} = \text{CONST}$$

- DENSITY OF SYNAPSES IN GRAY MATTER

$$\frac{NM}{V_g} = \text{CONST}$$

- DENSITY OF SHORT-RANGE AXONS IN GRAY MATTER

$$\frac{NL_1}{V_g} = \text{CONST}$$

- DENSITY OF LONG-RANGE AXONS IN WHITE MATTER

$$\frac{NL_2}{V_W} = \text{CONST}$$

N – # OF NEURONS IN CORTEX

M – # OF SYNAPSES PER NEURON

L_1 – SHORT-RANGE AXON LENGTH

L_2 – LONG-RANGE AXON LENGTH

V_g – GRAY MATTER VOLUME

V_W – WHITE MATTER VOLUME

$$V_W \sim V_g^{\gamma}$$

$$\gamma = 1.2 - 1.3$$

MORE CORTICAL INVARIANTS...

- THE RATIO OF THE NUMBER OF EXCITATORY TO INHIBITORY SYNAPSES

- CORTICAL MODULE SIZE

SCALING LAWS

SCALE TRANSFORMATIONS LEAVING THE ABOVE DENSITIES INVARIANT

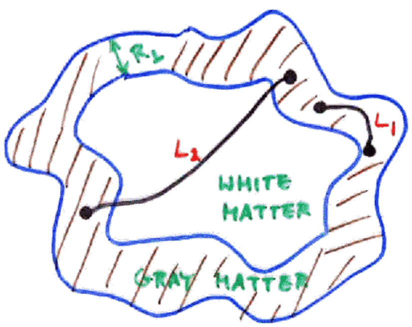
$$N \longrightarrow N(s) = Ns$$

$$M \longrightarrow M(s) = M s^{\alpha}$$

$$\boxed{\begin{aligned} L_1 &\longrightarrow L_1(s) = L_1 s^{\alpha} \\ L_2 &\longrightarrow L_2(s) = L_2 s^{\gamma(1+\alpha)-1} \end{aligned}}$$

$$R_\perp \longrightarrow R_\perp(s) = R_\perp s^{\alpha}$$

$$r \longrightarrow r(s) = r s^{1/2}$$



$$R_\perp \sim W^{\alpha}$$

AXON LENGTHS L_1, L_2 GROW EXPONENTIALLY WITH EXPONENT α FOR A GIVEN SCALE S.

MICROSCOPIC CONNECTIVITY

AVERAGE CONNECTIVITY BETWEEN NEURONS:

$$p = M/N$$

FROM THE ABOVE INVARIANTS AND USING THE FACT THAT: $N \sim V_g^{0.9}$ WE OBTAIN

$$p \sim V_g^{-0.8}$$

MICROSCOPIC CONNECTIVITY DECREASES QUICKLY WITH BRAIN SIZE!

EXAMPLE:

$$\frac{V_g(\text{human})}{V_g(\text{rat})} \simeq 615$$

$$\Downarrow$$

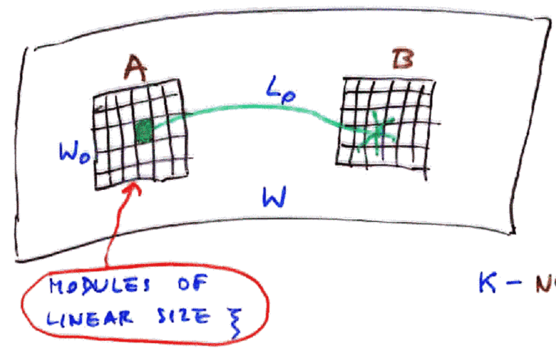
$$\frac{p(\text{human})}{p(\text{rat})} \simeq \frac{1}{170}$$

ANATOMICAL DATA SHOW THAT THERE IS SOME ORDER IN MACROSCOPIC CONNECTIONS BETWEEN CORTICAL AREAS, SUGGESTING THAT CORTEX AT LARGE SCALE IS FAR FROM BEING A HOMO-GENEOUS NETWORK.

$\rightsquigarrow$ INCLUDE IN CONSIDERATIONS:

AREAS, MODULES AND PATCHY PROJECTIONS.

CONNECTIVITY BETWEEN AREAS



K – NUMBER OF AREAS

PROBABILITY OF CONNECTION BETWEEN MODULE IN AREA A AND THE WHOLE AREA B:

$$\mathcal{H} = q \cdot \frac{W_0}{W} \cdot \frac{\pi L_0^2}{W}$$

q – PROBABILITY OF SENDING AXONS TO WHITE MATTER.

$\frac{W_0}{W}$ – PROB. THAT AXONAL BUNDLE TERMINATES IN B.

$\frac{\pi L_0^2}{W}$ – PROB. THAT AREA B CAN BE PHYSICALLY REACHED GIVEN FINITE AXONAL LENGTH L_0 IN WHITE MATTER.

PROBABILITY THAT AREA A CONNECTS B:

$$Q = 1 - (1-x)^{Nb/\xi^2} \simeq$$

$$\simeq 1 - \exp\left(-\frac{a q L_0^2}{\xi^2 K^2}\right)$$

EXPONENT IS AVERAGE NUMBER OF AXONAL BUNDLES CONNECTING AREAS A AND B

THIS FORMULA CAN HAVE PRACTICAL IMPORTANCE FOR ESTIMATION OF AVERAGE LENGTH OF AXONS IN WHITE MATTER:

- FOR RAT: $K=26$, $Q=0.25$ → $L_0 \simeq 4.7$ MM
- FOR CAT: $K=65$, $Q=0.27$ → $L_0 \simeq 12.4$ MM
- FOR MACAQUE: $K=73$, $Q=0.15$ → $L_0 \simeq 10.0$ MM

  SECOND INDEP. EVALUATION:

  $L_0 \simeq 12.0 - 17.0$ MM

SCALING OF BASIC CORTICAL CHARACTERISTICS WITH BRAIN SIZE

HOW DOES CONNECTIVITY Q BETWEEN CORTICAL AREAS DEPEND ON THE BRAIN SIZE?

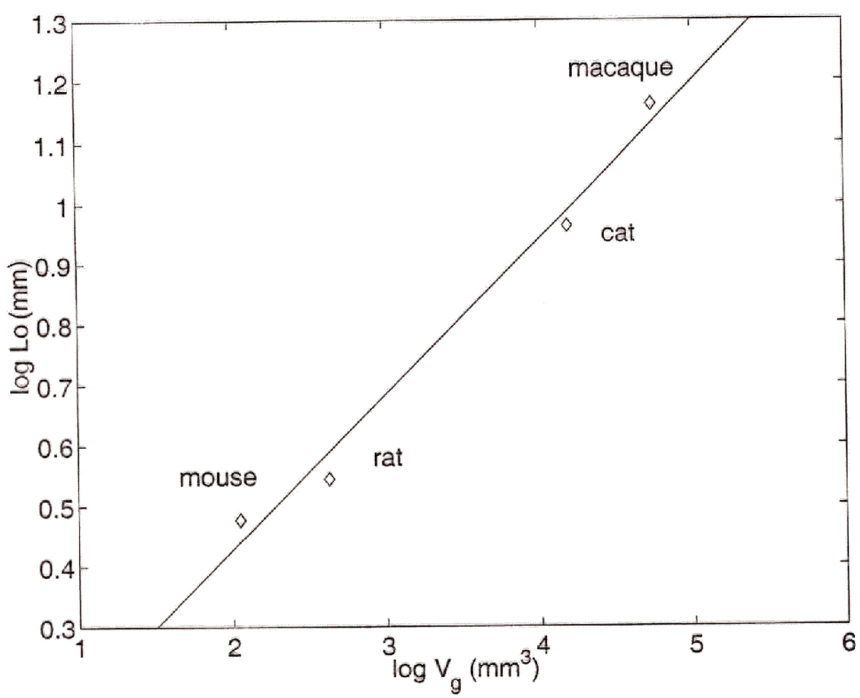
IT DEPENDS ON HOW L_0, K, q, ξ SCALE WITH THE BRAIN VOLUME.

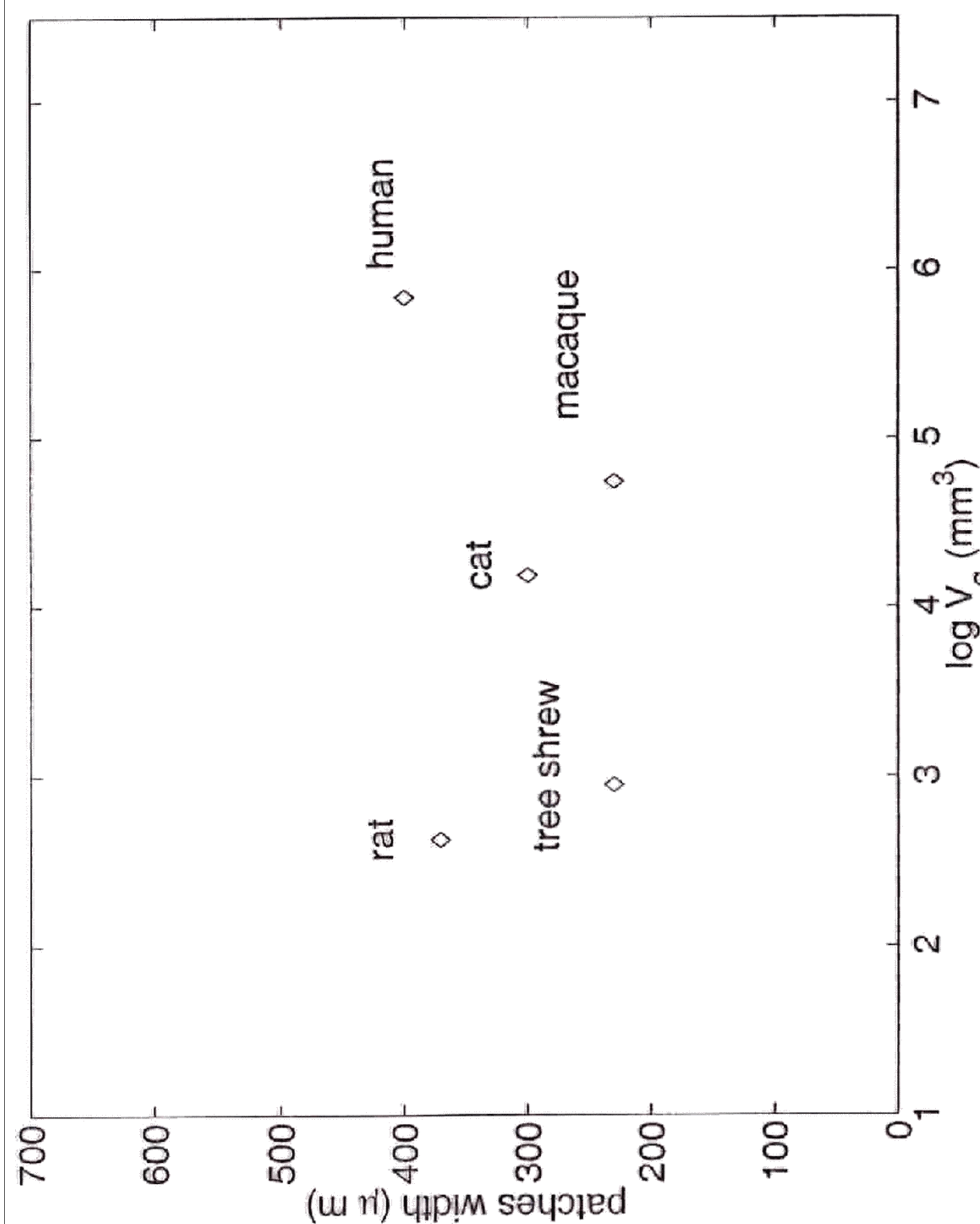
- NUMBER OF AREAS $K \sim V_g^{\alpha}$, $\alpha \simeq 0.4$ (CHANGIZI, 2001)
- $L_0 \sim V_g^{\beta}$, $\beta = 1/3$ (ZHANG + SEJNOWSKI '2000)

  $\beta = 0.41 - 0.44$ (CHANGIZI '2001)

  $\beta = 0.26$ (KARBOWSKI '2002)
- $\xi \sim$ PATCHES WIDTH $\sim V_g^0$ → INVARIANT
- $q \sim V_g^0$ → INVARIANT (INFERRED FROM DATA OF OLIVARES ET AL '2001 ON CORPUS CALLOSUM)

$$L_o = 1.10 \cdot V_g^{0.26}$$





SCALING OF AREA CONNECTEDNESS WITH BRAIN SIZE

$$Q = 1 - \exp\left(-A\, V_g^{\delta}\right)$$

WHERE

$\delta = 2(\beta - \bar{\alpha})$, A IS BRAIN SIZE INDEPEN. CONSTANT

- $\delta = -0.28$ FOR $\beta = 0.26$
- $\delta \simeq 0$ FOR $\beta \simeq 0.4$

AREA CONNECTEDNESS IS EITHER ONLY WEAKLY DEPENDENT OR INDEPENDENT OF THE BRAIN SIZE.

EXAMPLES OF TRADE-OFF

- LOCAL INFORMATION TRANSFER
- GLOBAL INFORMATION PROCESSING

BRAIN RESOURCES

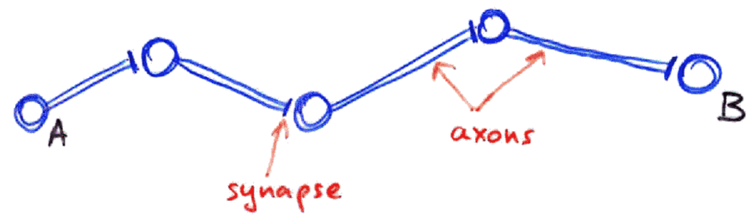
- BELIEF THAT CEREBRAL CORTEX IS DESIGNED IN SUCH A WAY AS TO SAVE LIMITED BIOCHEMICAL RESOURCES (CAYAL '11).
- AXONS (WIRE) – PRIME TARGET OF SAVING IN THE BRAIN, SINCE THEY ARE IMPORTANT IN LONG DISTANCE COMMUNICATION BETWEEN AREAS.
- PRINCIPLE OF MINIMAL AXON LENGTH: CANDIDATE FOR AN OPTIMAL WIRING (MITCHISON '91, CHERNIAK '95, VAN ESSEN '97)

PROBLEM

- THE PRINCIPLE OF MINIMAL AXON LENGTH DOES NOT TAKE INTO ACCOUNT ENERGETIC CONSTRAINTS INVOLVED IN INFORMATION TRANSFER OVER LONG DISTANCES.

HOW TO MEASURE ENERGETIC COST?

- ENERGETIC (METABOLIC) COST OF INFORMATION TRANSFER BETWEEN NEURONS A AND B IS PROPORTIONAL TO THE AVERAGE NUMBER OF STEPS NEEDED TO CONNECT A AND B.



METABOLIC COST OF INFORMATION TRANSFER $\sim$ AVERAGE DEGREE OF SEPARATION BETWEEN NEURONS.

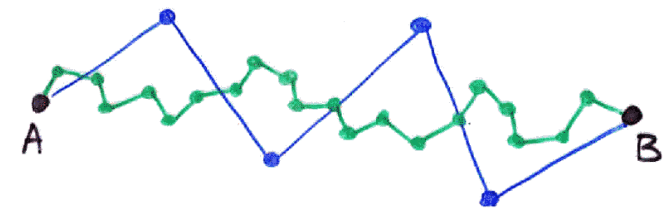
OPTIMAL WIRING

- AXON LENGTH → BIOCHEMICAL COST
- DEGREE OF SEPARATION BETWEEN NEURONS → ENERGETIC COST

OPTIMAL WIRING: BOTH AXONAL LENGTH AND AVERAGE DEGREE OF SEPARATION BETWEEN NEURONS SHOULD BE AS SMALL AS POSSIBLE.

"IF YOU SAVE ON SOMETHING YOU LOSE ON SOMETHING ELSE"

- AXON LENGTH AND THE DEGREE OF SEPARATION BETWEEN NEURONS ARE INVERSELY PROPORTIONAL.



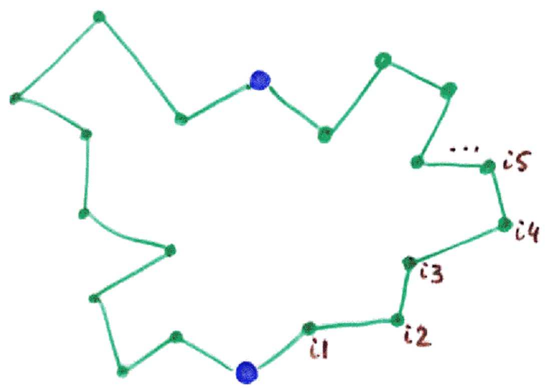
SMALLER AXON LENGTH ⇒ LARGER THE DEGREE OF SEPARATION AND VICE VERSA

↓

SMALLER BIOCHEMICAL COST ⇒ LARGER METABOLIC COST OF INFORMATION TRANSFER AND VICE VERSA.

DEGREE OF SEPARATION

$S_k(r)$ – PROBABILITY OF k-STEP CONNECTION BETWEEN NEURONS SEPARATED BY r VIA AT LEAST ONE PATH



$$S_k(r) = 1 - \prod_{\langle i1,\dots,ik-1\rangle}^{N_k} \left\{ 1 - p(\vec{r}_{i_1})\, p(\vec{r}_{i_2}-\vec{r}_{i_1}) \dots p(\vec{r}-\vec{r}_{i_{k-1}}) \right\}$$

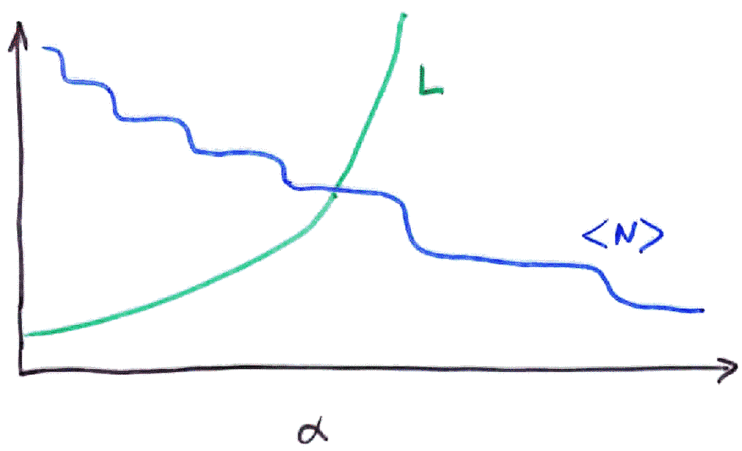
$N_k = \binom{N-2}{k-1}(k-1)!$ – NUMBER OF ALL POSSIBLE PATHS CONNECTING 2 NEURONS IN k-STEPS

$$S_k(r(s), s) \xrightarrow{s\to\infty} \begin{cases} 1, & k > 1/\alpha \\ 0, & k < 1/\alpha \end{cases}$$

THE SMALLEST NUMBER OF STEPS NEEDED TO CONNECT 2 NEURONS IS $\left[\frac{1}{\alpha}+1\right]$

THE AVERAGE DEGREE OF SEPARATION $\langle N \rangle_\infty$ IN THE LIMIT OF INFINITE NETWORK IS GIVEN BY THE SMALLEST INTEGER SATISFYING $\langle N \rangle_\infty > \frac{1}{\alpha}$.

CONCLUSION



IF YOU MINIMIZE THE DEGREE OF SEPARATION YOU MAXIMIZE AXONAL LENGTH AND VICE VERSA.

TRADE-OFF

PLATEAUS — IN $\langle N \rangle$ MAY REDUCE THE COST OF FIBER LENGTH L.

EFFICIENT COMPUTATION IN CORTEX

ONE OF THE MAIN OBJECTIVES BRAINS TRY TO ACCOMPLISH IS TO PROCESS VARIOUS FORMS OF INFORMATION. THIS GOAL CAN BE ACHIEVED BY POSSESSING A CERTAIN LEVEL OF COMPUTATIONAL POWER. IF WE FOCUS ON COARSE-GRAINED MACROSCOPIC DESCRIPTION THEN FEW FUNCTIONAL/ARCHITECTONIC PRINCIPLES CAN BE IDENTIFIED WHICH BRAINS HAVE TO MEET TO EFFICIENTLY PROCESS INFORMATION:

- NUMBER OF AREAS SHOULD INCREASE AS QUICKLY AS POSSIBLE WITH THE BRAIN SIZE.
- BRAINS SHOULD TRY TO MAINTAIN A CONSTANT AREA CONNECTEDNESS REGARDLESS OF THEIR SIZE.
- INTRA- AND INTER-HEMISPHERIC TEMPORAL DELAY SHOULD NOT INCREASE WITH BRAIN SIZE.

$$\tau \sim \frac{L_0}{v} \sim \frac{L_0}{d}$$ ← AXON DIAMETER

CONFLICTING CONSTRAINTS

· FROM WHITE MATTER VOLUME:

$$V_w \sim N L_o d^2$$

WHITE/GRAY MATTER RATIO

$$\boxed{\frac{V_w}{V_g} \sim V_g^{-0.1} \frac{K^3 Q^{3/2}}{\tau^2}}$$

IF THE ABOVE 3 HYPOTHETICAL GLOBAL FUNCTIONAL PRINCIPLES WERE SATISFIED SIMULTANEOUSLY, THEN THE WHITE MATTER VOLUME WOULD HAVE TO GROW EXCESSIVELY WITH GRAY MATTER DUE TO FAST GROWTH OF K^3 WITH BRAIN SIZE.

BETTER STRATEGY TO OPTIMIZE TRADE-OFF:

TO REDUCE EXCESSIVE SCALING V_w WITH V_g:

- SLOWER INCREASE OF K WITH BRAIN SIZE
- SLOW INCREASE OF τ WITH BRAIN SIZE
- SLOW DECREASE OF Q WITH BRAIN SIZE

SUCH STRATEGY SEEMS TO BE TAKEN BY BRAIN DEVELOP, SINCE ...

$$\tau \sim L_o/d \sim V_g^{0.2}$$

$$Q \sim V_g^{-0.28}$$

THIS COMPROMIZE MIGHT LEAD TO SLIGHT DECREASE IN INFORMATION-PROCESSING CAPABILITIES OF THE BRAIN AS IT GETS BIGGER ...

METABOLIC COST OF THE WHOLE CORTEX

HOW MANY SYNAPSES IS ACTIVE AT RESTING CONDITIONS ?

$$E \sim f N M \sim f V_g$$

ENERGY

FRACTION OF EXCITAT. SYNAPSES

$$E \sim V_g \cdot V_{body}^{-0.15} \sim V_g^{0.8}$$ (HOFMAN, 1983)

$$f \sim V_g^{-0.2}$$

AS BRAIN GETS BIGGER RELATIVELY LESS SYNAPSES IS ACTIVE !

SUMMARY

ARCHITECTURE AND SIZE OF THE CEREBRAL CORTEX ARE SHAPED BY DIFFERENT CONSTRAINTS WITH CONFLICTING OUTCOMES.

DESPITE THIS COMPETING CONSTRAINTS, EVOLUTION HAS FOUND WAYS TO DEVELOP FUNCTIONAL BRAINS, WHICH REPRESENT A BALANCED DESIGN THAT IS IN SOME SENSE OPTIMAL.