Neural reuse in the evolution and development of the brain

Michael L. Anderson

Department of Psychology
Franklin & Marshall College
Lancaster, PA USA

Institute for Advanced Computer Studies
Program in Neuroscience and Cognitive Science
University of Maryland
College Park, MD USA

Where we are

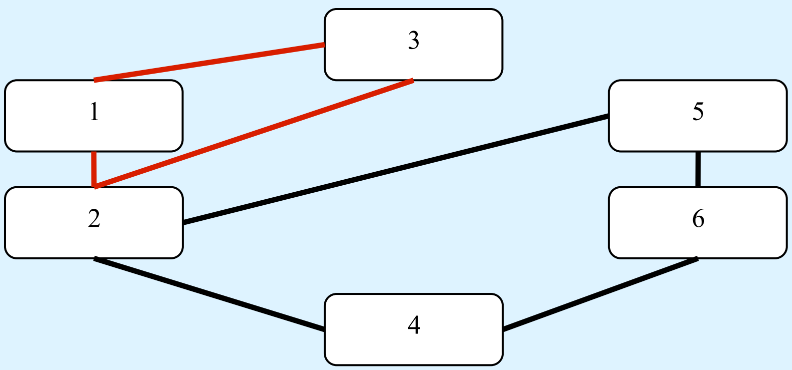
20+ years of efforts in non-invasive functional brain imaging

+

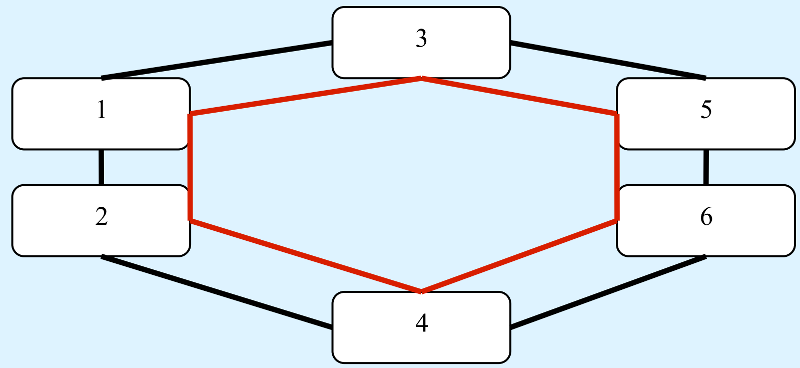
Tens of thousands of studies =

A huge scientific opportunity to revisit some of the “big” questions

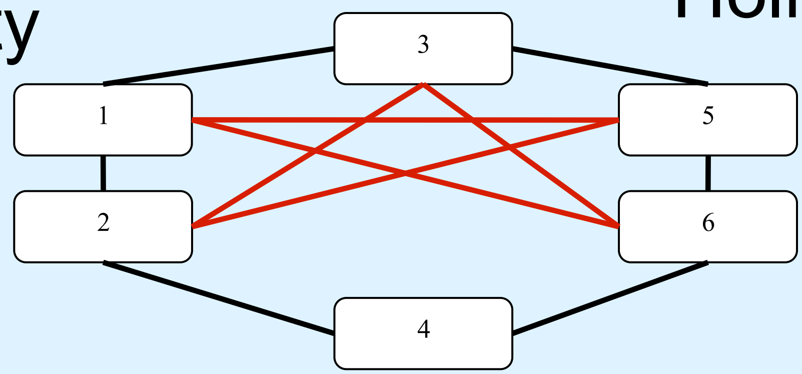
Overall functional architecture



Modularity

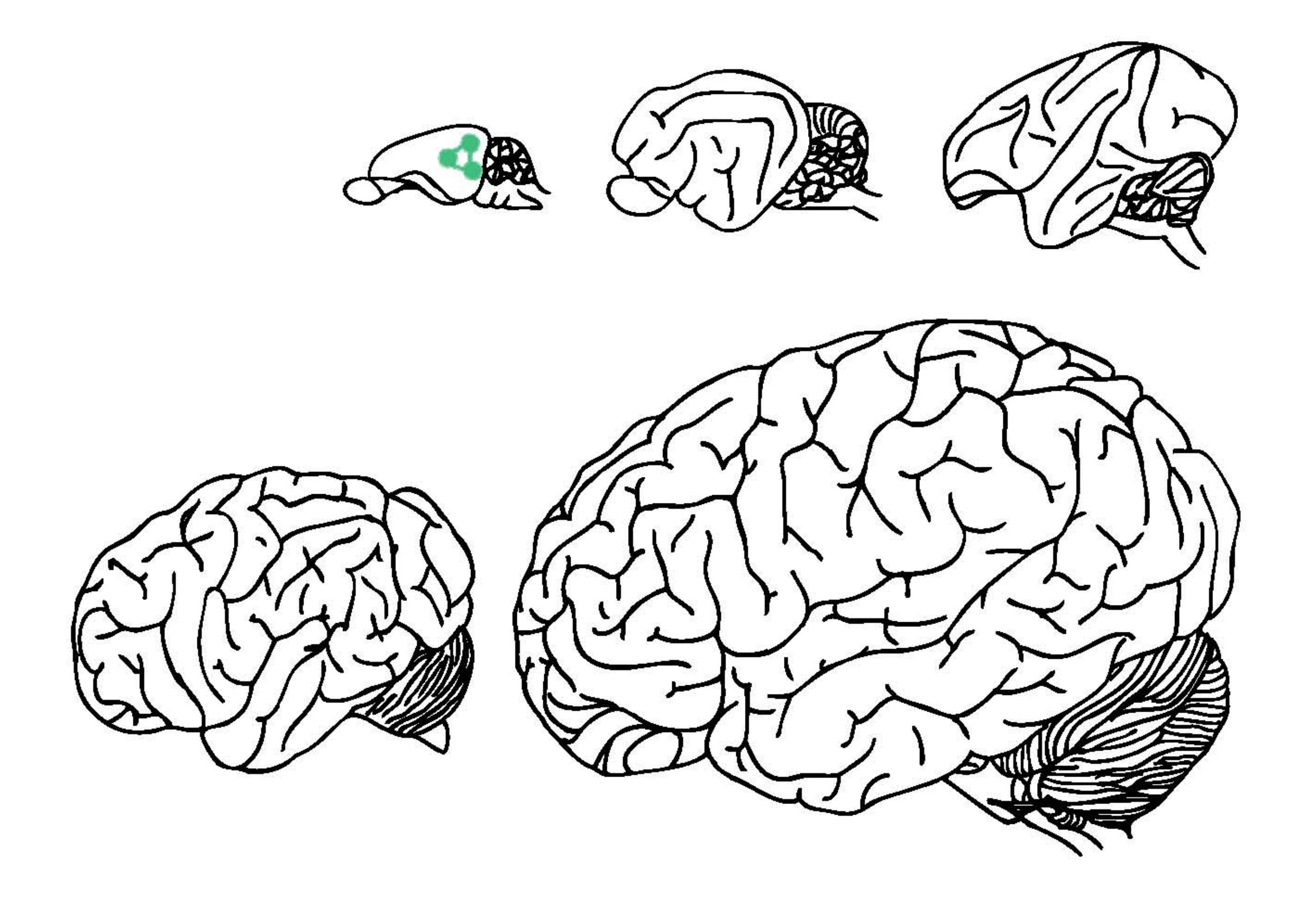


Holism / PDP

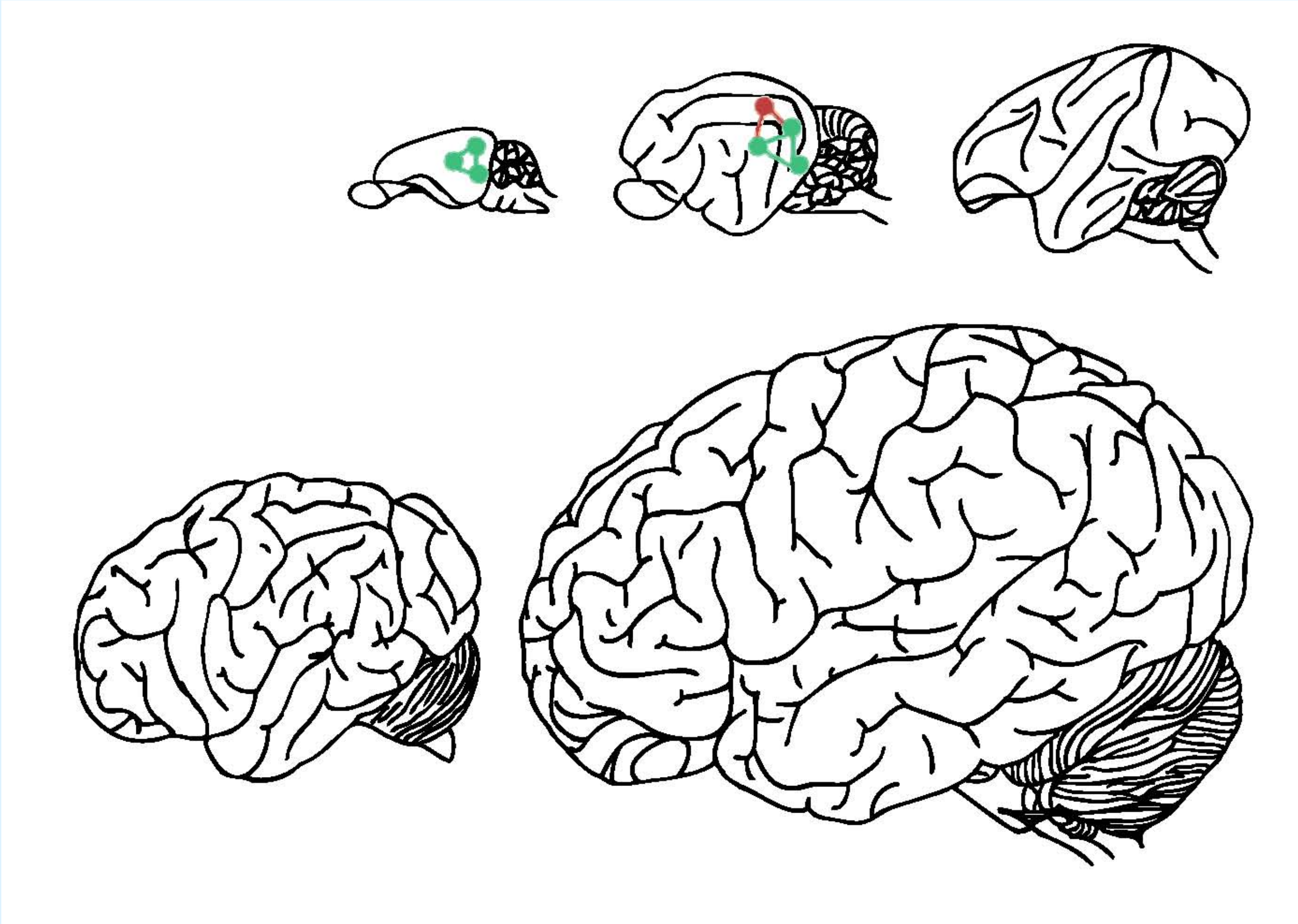


Reuse

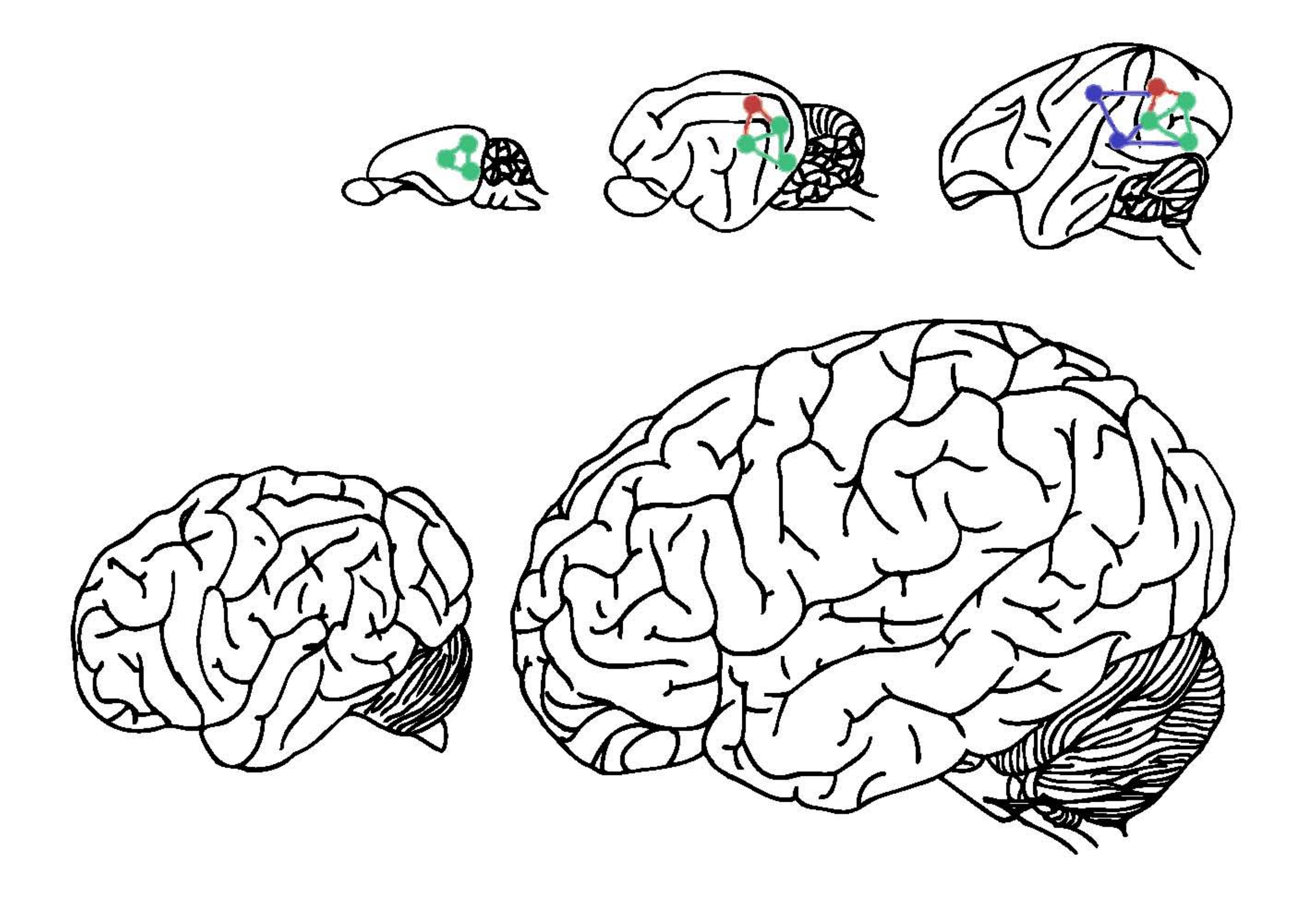
How did the brain evolve?



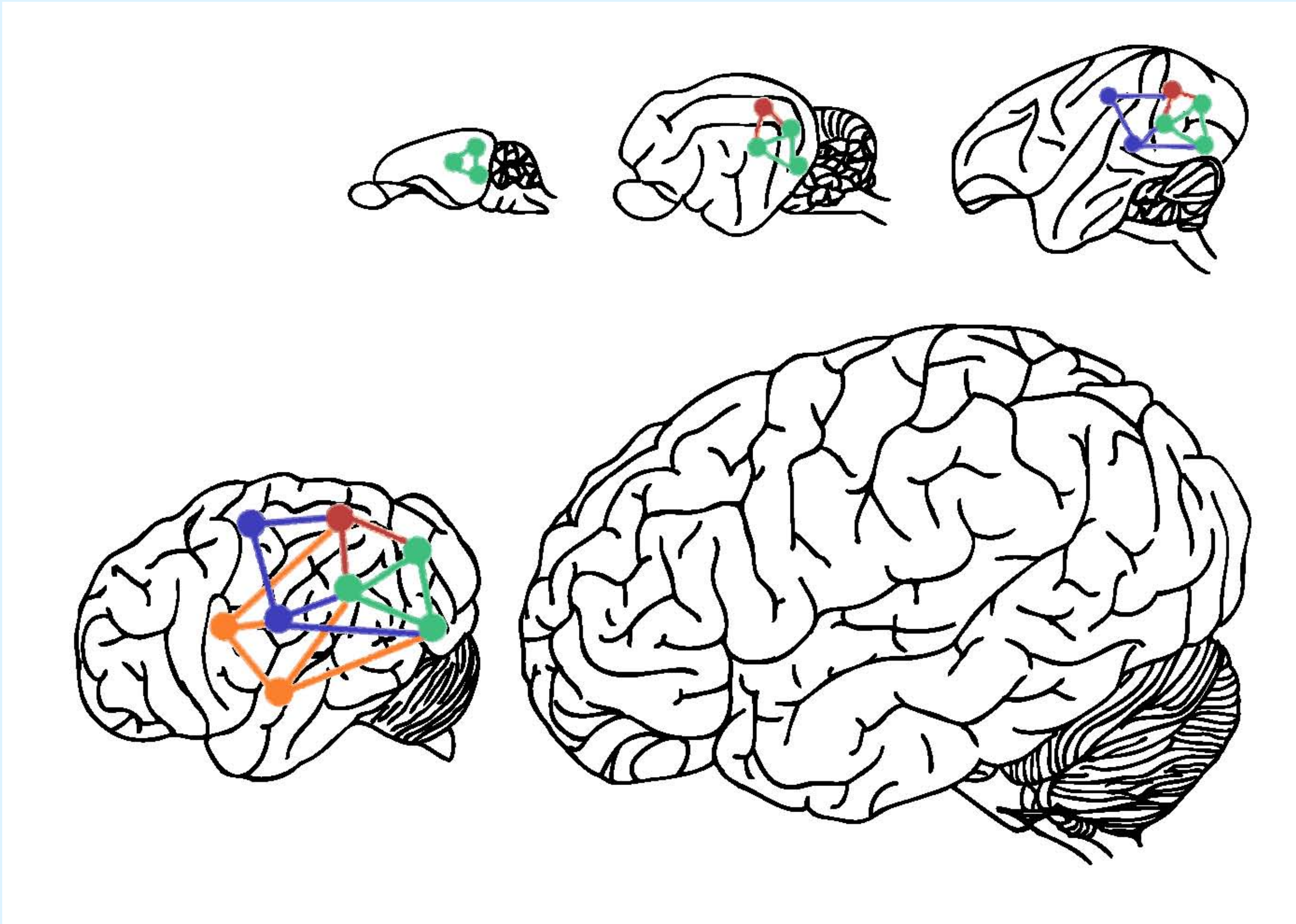
How did the brain evolve?



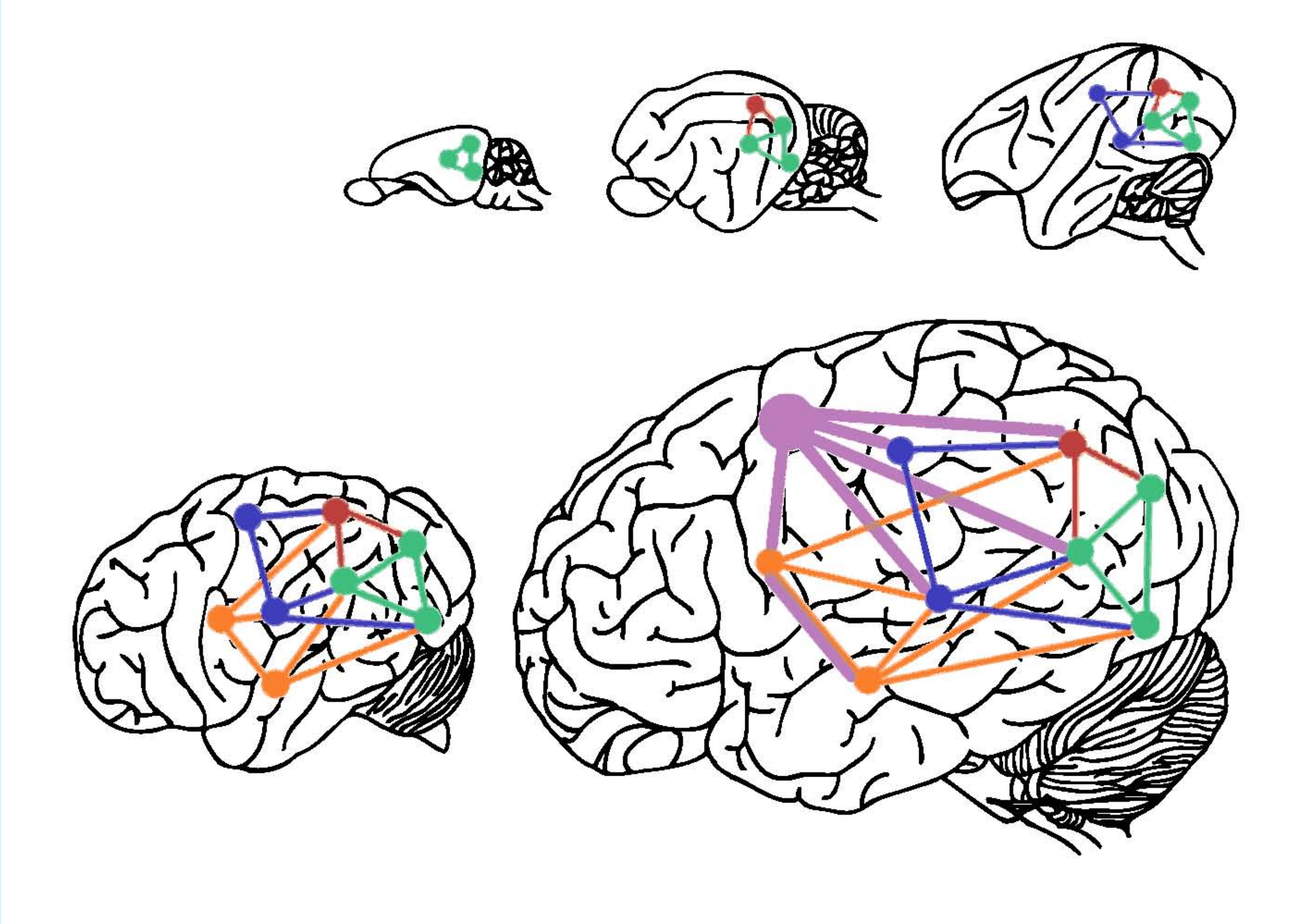
How did the brain evolve?



How did the brain evolve?



How did the brain evolve?



How did the brain evolve?

Notice what's happening:

- New functions develop by incorporating parts used in existing functions.
- Over time, many local circuits get reused in different cognitive functions.
- That reuse may be in different cognitive domains

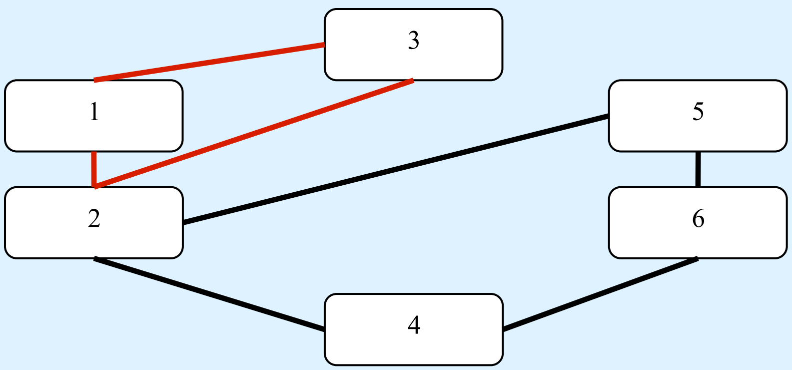
How did the brain evolve?

This is a “component reuse” or “***building-block***” model of brain evolution.

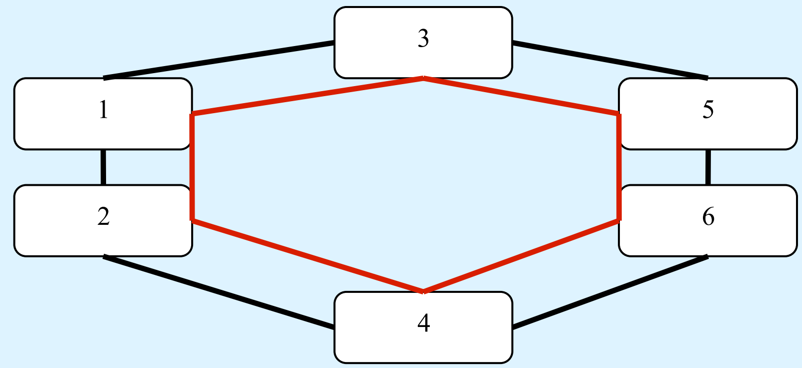
Components evolved for one cognitive purpose are “exapted” for later uses.

However, the original functionality is not lost (reuse not driven by plasticity)

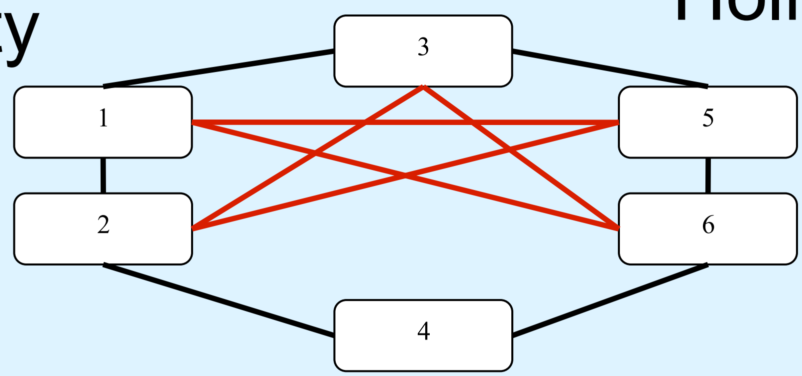
Overall functional architecture



Modularity



Holism / PDP



Reuse

Empirical implications

Neural reuse means that:

I. Local neural circuits are typically redeployed in support of multiple cognitive functions, across traditional task-domain boundaries

Empirical implications

II. Redeployed circuits will have the same “working” (but a different “use”) in each of the functional complexes they support

Empirical implications

III. Task domains will differentially activate not ***regions***, but ***networks***

Interactions between regions will be a better indication of function than _actions of_ regions

Empirical implications

IV. More recent cognitive functions will utilize more, and more widely scattered local circuits

Neural reuse

I. Local circuits are typically redeployed in support of multiple cognitive functions across traditional task-domain boundaries

II. Redeployed circuits have the same “working” in each of the functional complexes they support

III. Task domains will be differentiated at the network level

IV. More recent cognitive functions will utilize more, and more widely scattered local circuits

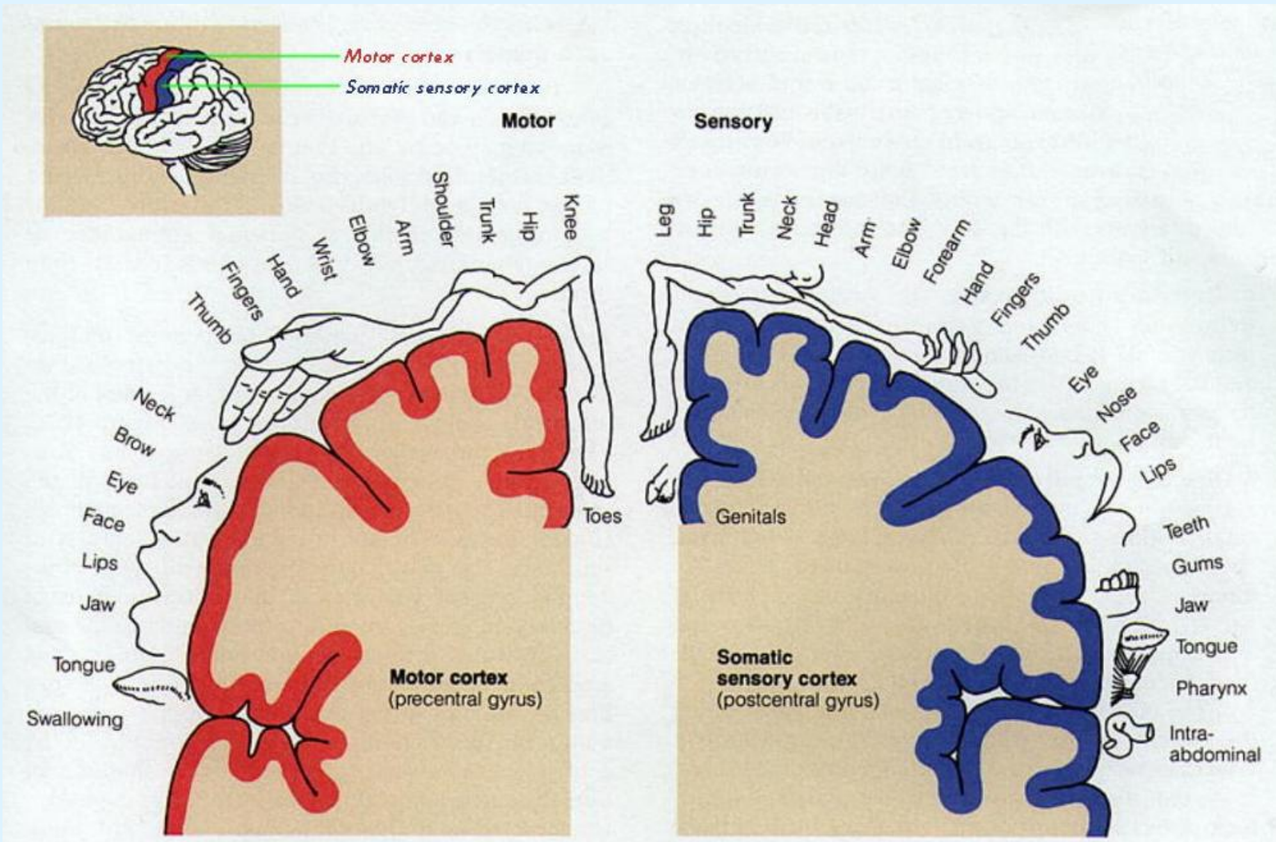
Implication I: Selectivity

The primary guiding idealization of the functional organization of the brain for at least 50 years.

Brain regions selectively respond to

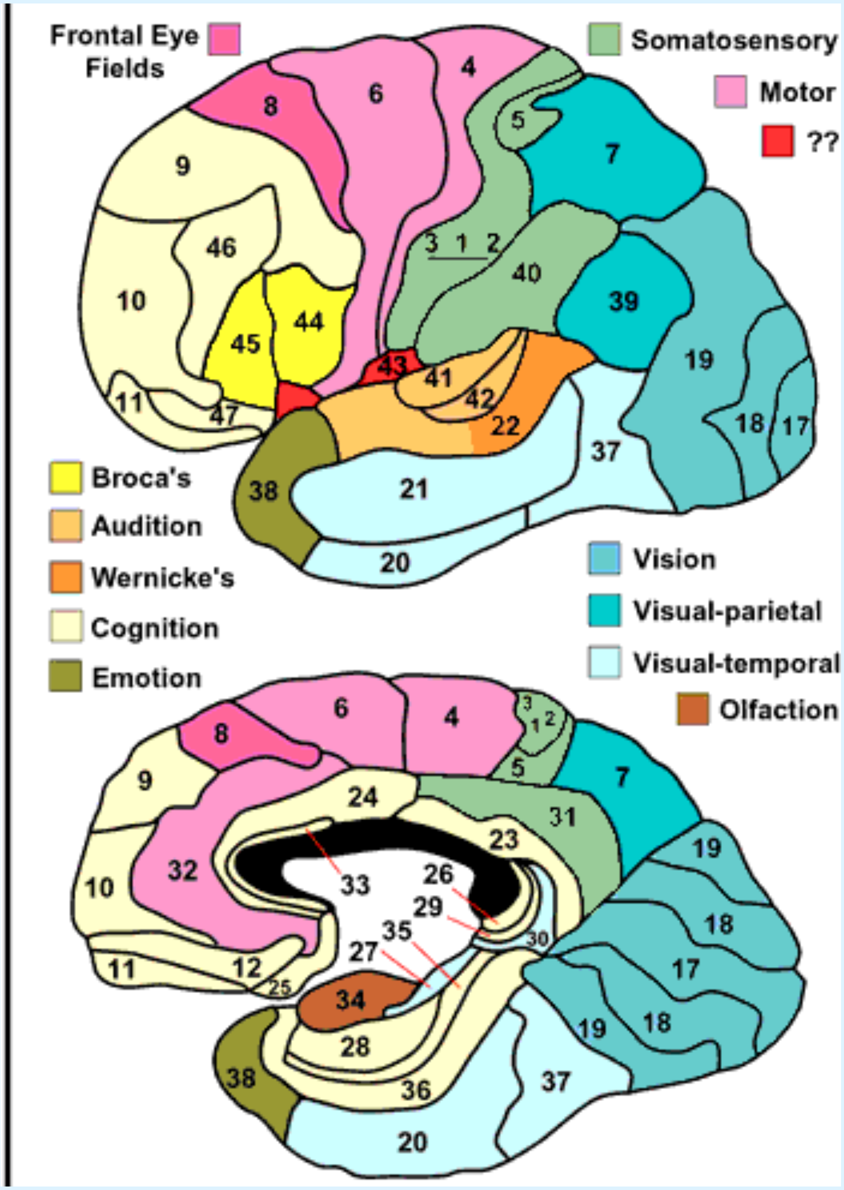
- Specific input classes
- Tasks and task categories

Functional Selectivity



Penfield’s Homunculus, 1954

Domain Selectivity



Brodmann map showing functional domains

NICAM Database

NICAM database contains:

- **2,603** experiments from **824** journal articles investigating over **70** different task domains
- **21,553** regional activations
- Only: Whole-brain analysis, post-subtraction activations

Empirical Review of Imaging Experiments

Investigated 11 task domains:

- three action domains (execution, inhibition and observation)
- two perceptual domains (vision and audition)
- six "cognitive" domains (attention, emotion, language, working memory, semantic memory and reasoning).

Empirical Review of Imaging Experiments

Gives 1,469 experiments collectively reporting 10,701 eligible activations.

Procedure:

1. divide the brain into regions
2. assign each activation to a region.
3. measure the diversity of activations

Diversity measure

- Borrowed from the Census bureau

$$DV = \sqrt{\frac{\sum_{i=1}^{k} \left(Cat_i - mean\right)^2}{k}}$$

Results with 66 cortical + 12 sub-cortical

Overall average diversity: **0.70 (sd 0.12)**

Overall cortical diversity: **0.71 (sd 0.11)**

Overall sub-cortical diversity **0.63 (sd 0.17)**

Regions active in an average of ***95*** tasks across ***9*** different domains

Results with 66 cortical + 12 sub-cortical

Putting that in terms of ratio of posterior to prior probability (Poldrack 2006):

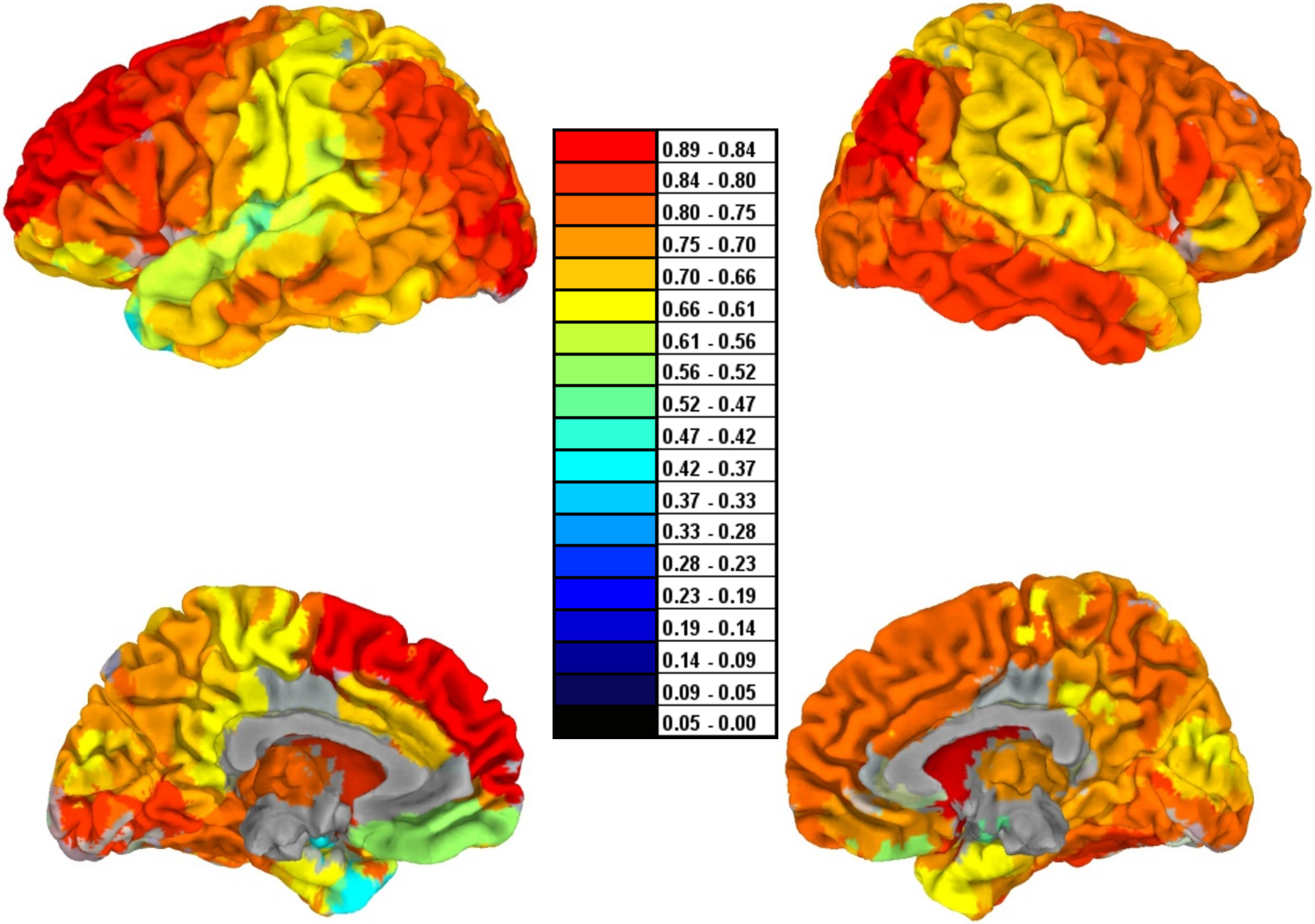
Average Bayes factor = 1.26

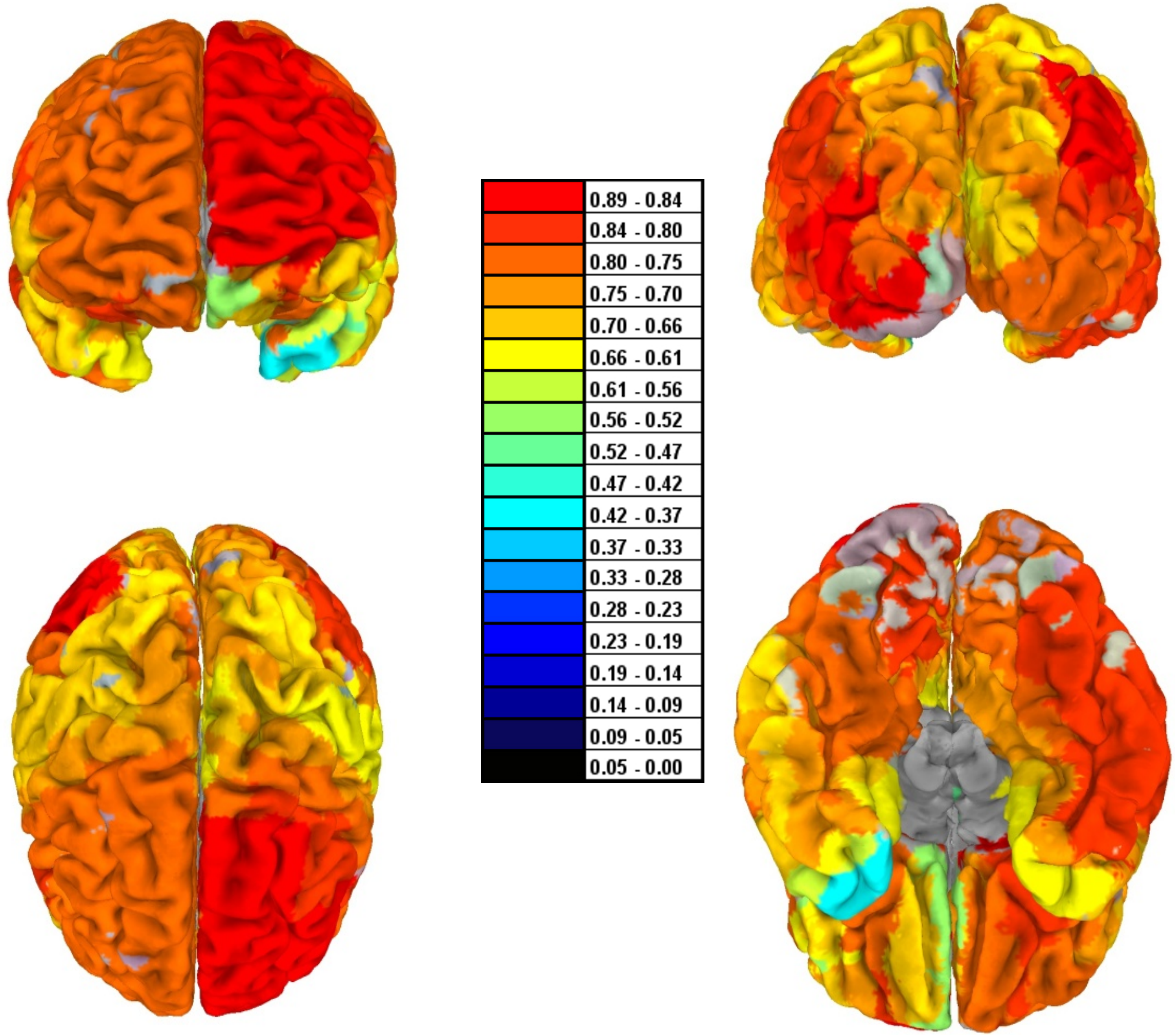
Even the ***best*** evidence is fairly weak: average MAX Bayes factor = 3.14

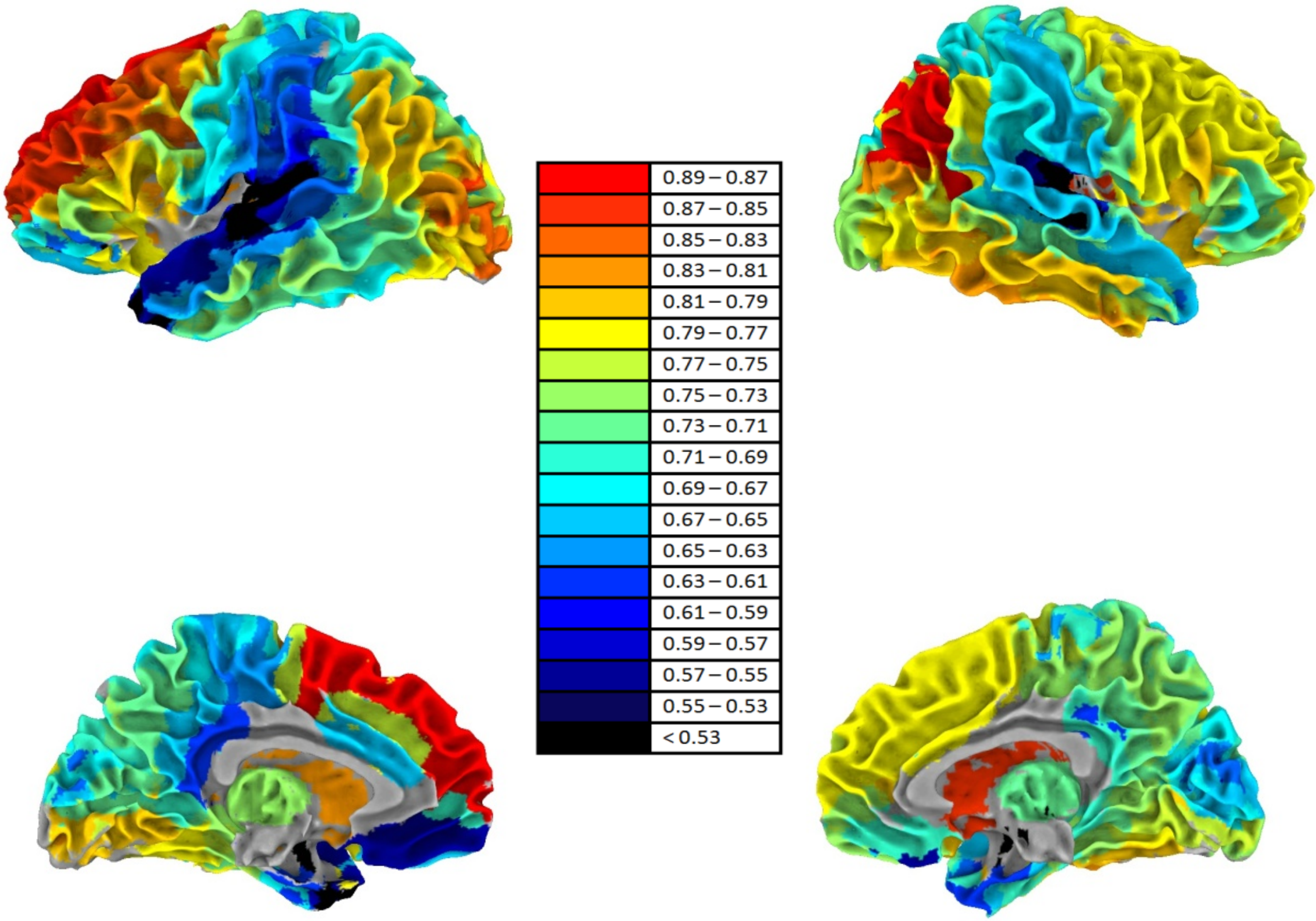
(and this presumes you know what the best evidence is)

Left inferior temporal cortex has a diversity of 0.70

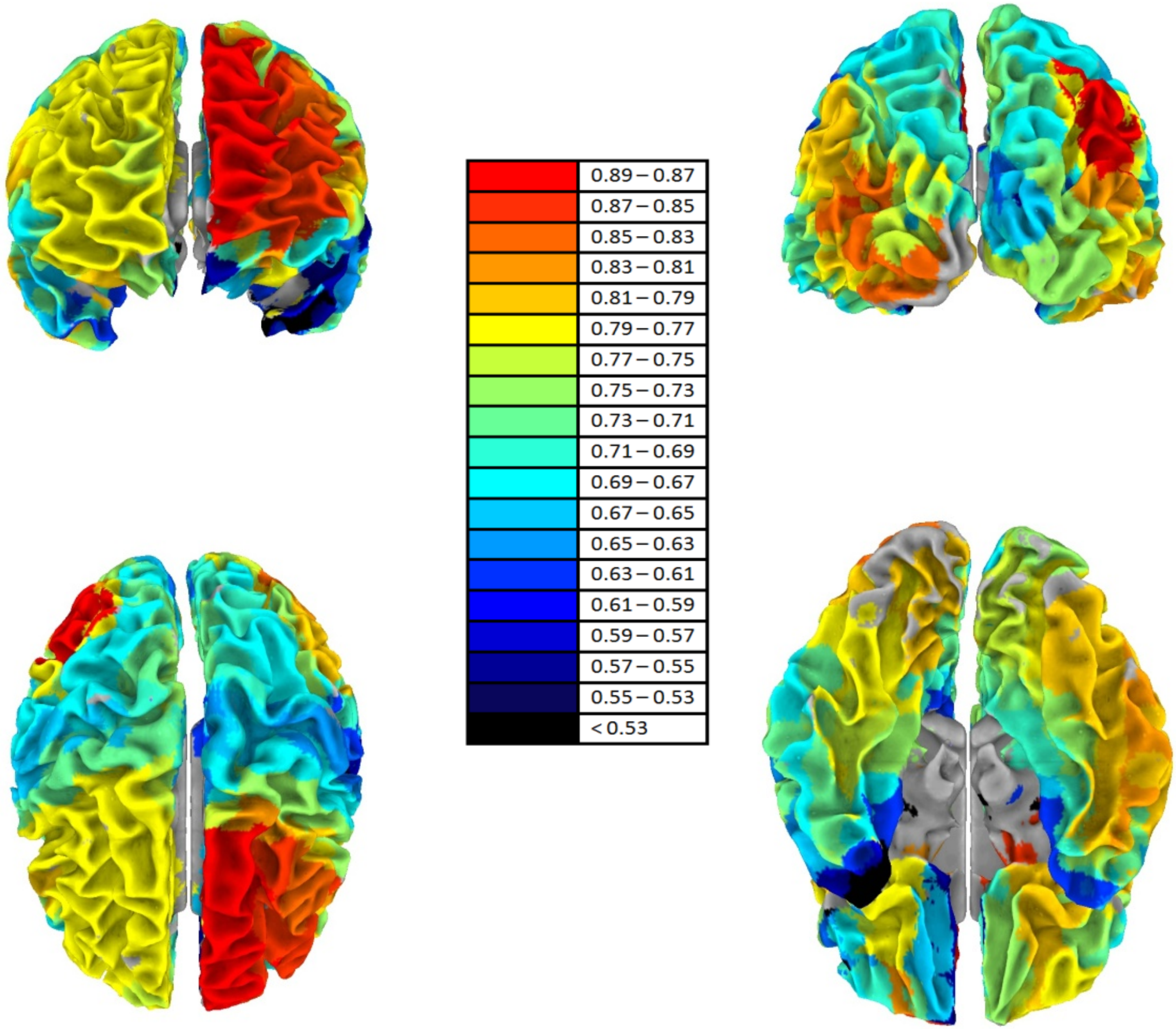
Domain	Proportion of activations
Action execution	0.06
Action imagination	0.06
Action inhibition	0.00
Visual perception	0.07
Audition	0.02
Attention	0.02
Semantic memory	0.12
Working memory	0.12
Emotion	0.06
Reasoning	0.12
Language	0.34


0.89 - 0.84
0.84 - 0.80
0.80 - 0.75
0.75 - 0.70
0.70 - 0.66
0.66 - 0.61
0.61 - 0.56
0.56 - 0.52
0.52 - 0.47
0.47 - 0.42
0.42 - 0.37
0.37 - 0.33
0.33 - 0.28
0.28 - 0.23
0.23 - 0.19
0.19 - 0.14
0.14 - 0.09
0.09 - 0.05
0.05 - 0.00


0.89 - 0.84
0.84 - 0.80
0.80 - 0.75
0.75 - 0.70
0.70 - 0.66
0.66 - 0.61
0.61 - 0.56
0.56 - 0.52
0.52 - 0.47
0.47 - 0.42
0.42 - 0.37
0.37 - 0.33
0.33 - 0.28
0.28 - 0.23
0.23 - 0.19
0.19 - 0.14
0.14 - 0.09
0.09 - 0.05
0.05 - 0.00



0.89 – 0.87
0.87 – 0.85
0.85 – 0.83
0.83 – 0.81
0.81 – 0.79
0.79 – 0.77
0.77 – 0.75
0.75 – 0.73
0.73 – 0.71
0.71 – 0.69
0.69 – 0.67
0.67 – 0.65
0.65 – 0.63
0.63 – 0.61
0.61 – 0.59
0.59 – 0.57
0.57 – 0.55
0.55 – 0.53
< 0.53


0.89 – 0.87
0.87 – 0.85
0.85 – 0.83
0.83 – 0.81
0.81 – 0.79
0.79 – 0.77
0.77 – 0.75
0.75 – 0.73
0.73 – 0.71
0.71 – 0.69
0.69 – 0.67
0.67 – 0.65
0.65 – 0.63
0.63 – 0.61
0.61 – 0.59
0.59 – 0.57
0.57 – 0.55
0.55 – 0.53
< 0.53

With 998 cortical + 54 sub-cortical
Results for 574 + 21 with > 5 activations

Overall average diversity: **0.52 (sd 0.13)**

Overall cortical diversity: **0.52 (sd 0.13)**

Overall sub-cortical diversity **0.59 (sd 0.12)**

Regions active in an average ***10*** tasks
over ***4*** different domains

Results with 998 cortical + 54 sub-cortical

Putting that in terms of ratio of posterior to prior probability (Poldrack 2006):

Average Bayes factor = 2.72

Even the ***best*** evidence is only moderately strong: average MAX Bayes factor = 5.54

(and this presumes you know what the best evidence is)

Sub-region of right supramarginal gyrus with diversity of 0.52

Domain	Proportion of activations
Action execution	**0.27**
Action imagination	**0.42**
Action inhibition	0.00
Visual perception	0.00
Audition	0.00
Attention	0.00
Semantic memory	0.00
Working memory	**0.11**
Emotion	0.00
Reasoning	**0.20**
Language	0.00

Selectivity

Provisional conclusion I:

Local circuits typically support multiple cognitive functions across traditional task-domain boundaries

Neural reuse

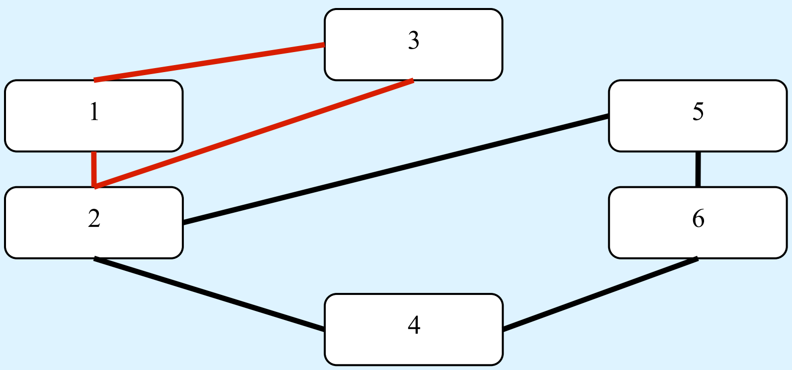
I. Local circuits are typically redeployed in support of multiple cognitive functions across traditional task-domain boundaries

II. Redeployed circuits have the same “working” in each of the functional complexes they support

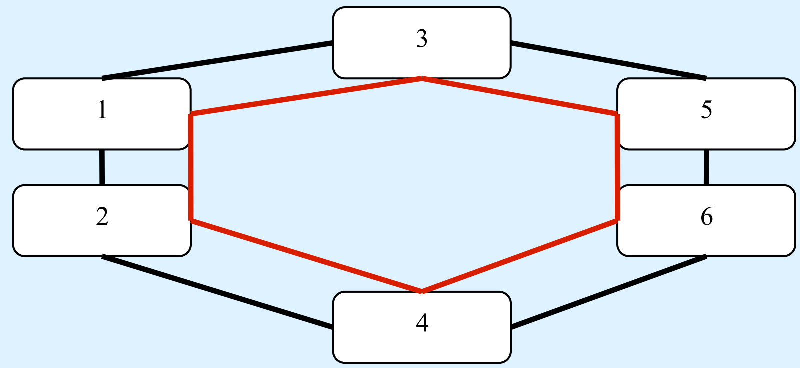
III. Task domains will be differentiated at the network level

IV. More recent cognitive functions will utilize more, and more widely scattered local circuits

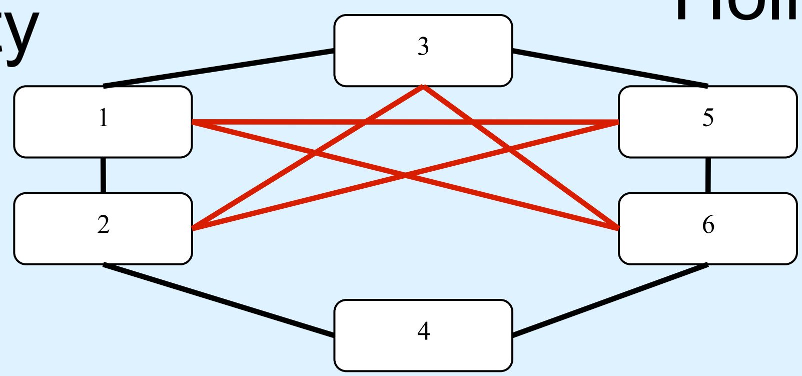
Overall functional architecture



Modularity



Holism / PDP



Reuse

Neural reuse

I. Local circuits are typically redeployed in support of multiple cognitive functions across traditional task-domain boundaries

II. Redeployed circuits have the same “working” in each of the functional complexes they support

III. Task domains will be differentiated at the network level

IV. More recent cognitive functions will utilize more, and more widely scattered local circuits

III: Networks or regions?

- “Functional connectivity” analysis of the same data set.
- Only 10 domains – insufficient data for functional connectivity study of action inhibition

Functional connectivity

1) Calculate chance probability (***Q***) of co-activation for each BA pair
2) In each domain, determine observed probability (***K***) of co-activation of each BA pair
3) Where there is a significant difference between ***Q*** and ***K*** (X^2), this is considered a "functional connection"

Functional architecture

The results of functional connectivity analyses can be represented as graphs

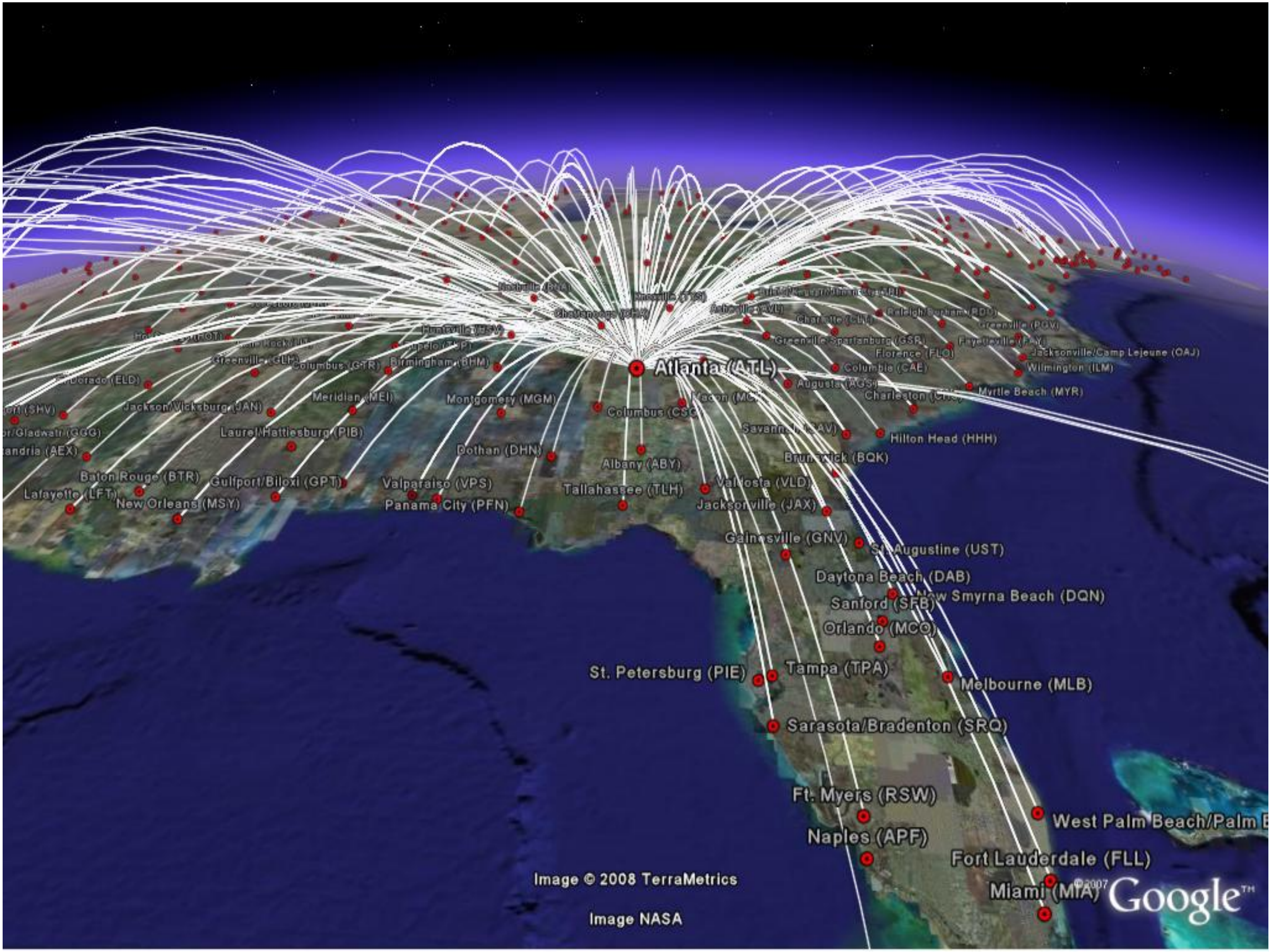
What's a graph?

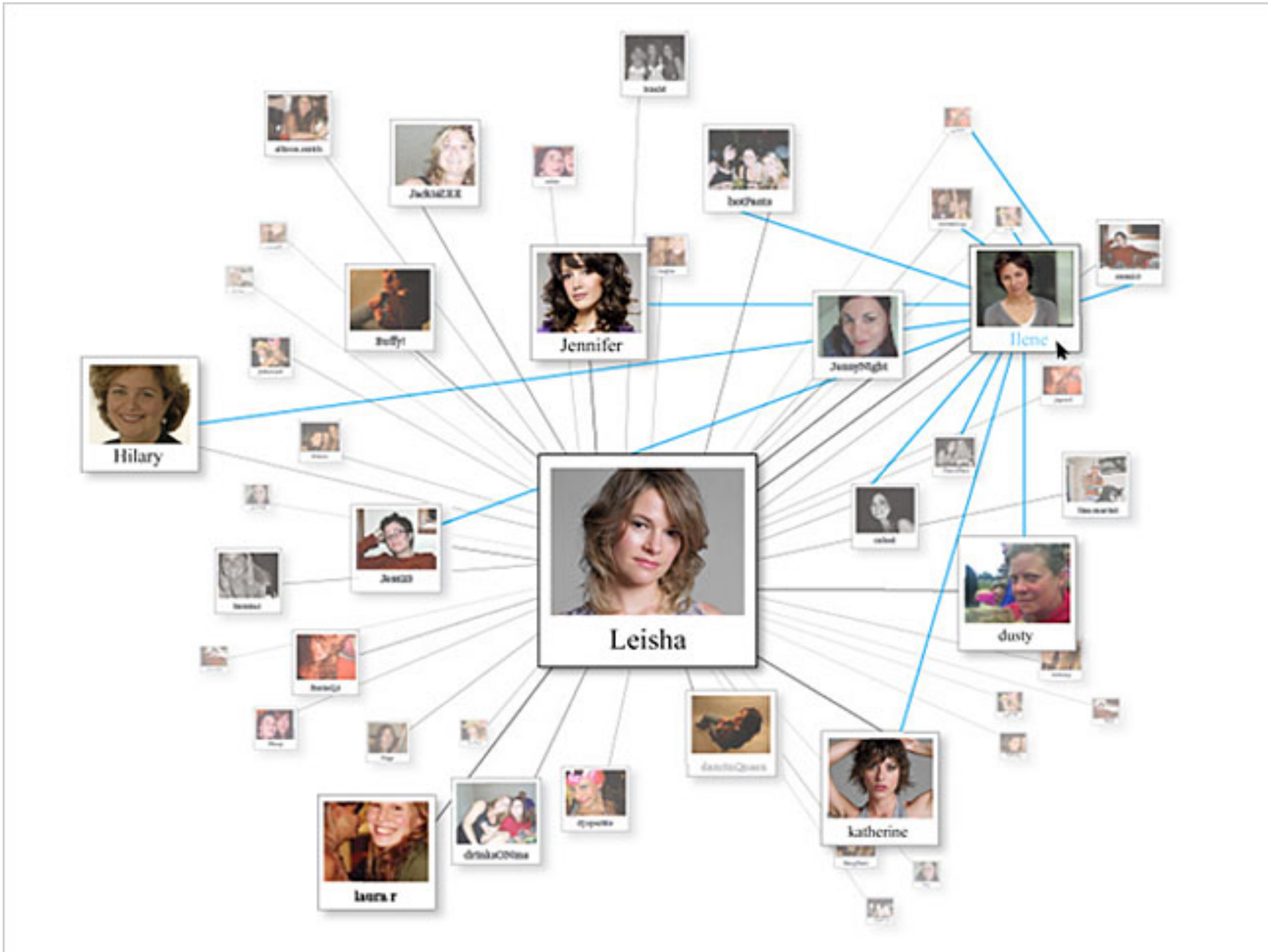
Graphs and graph theory

Graph: a set of “nodes” joined by “edges”

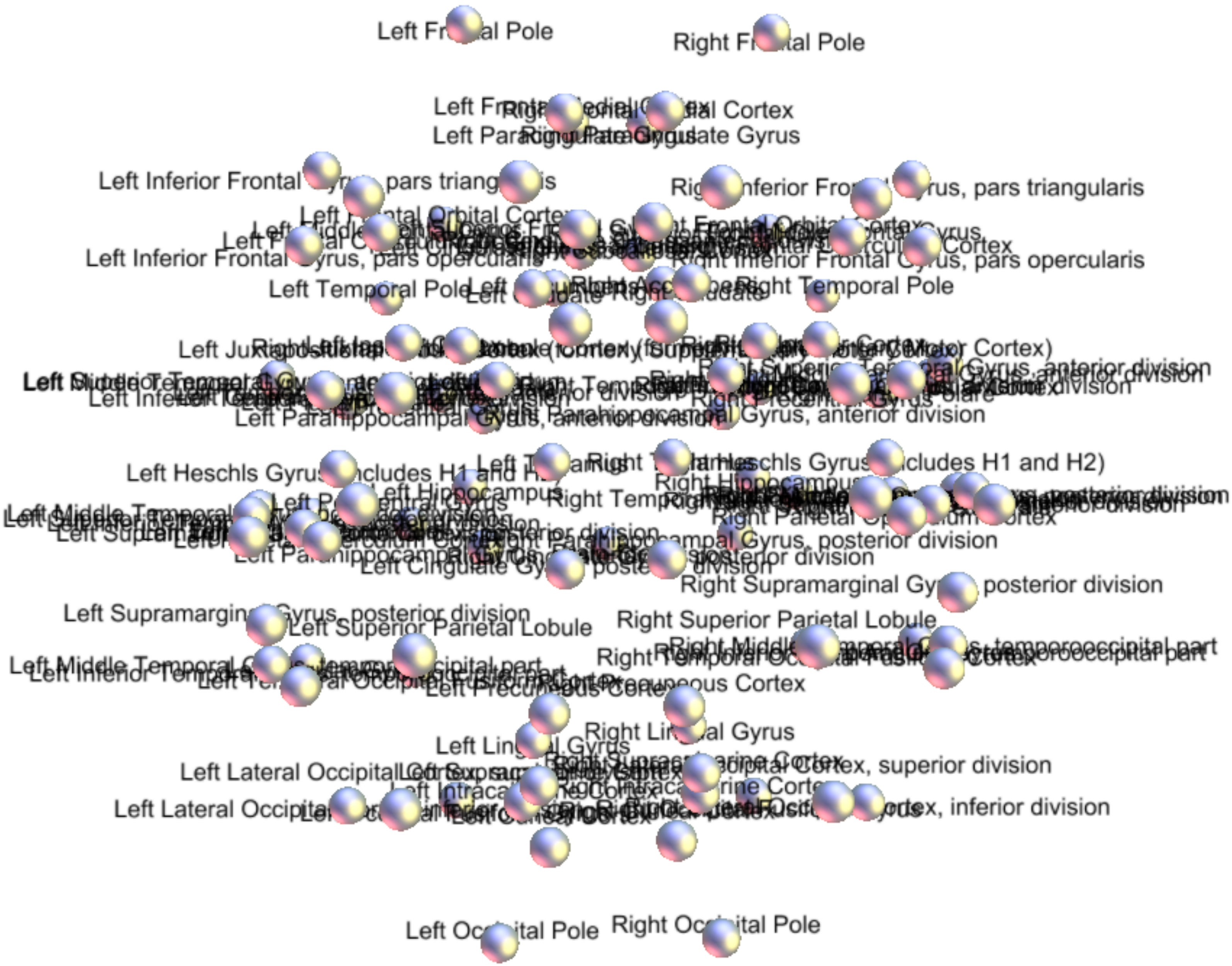
Examples:

- Airline route map
- Social network
- Website map
- Brain adjacency map

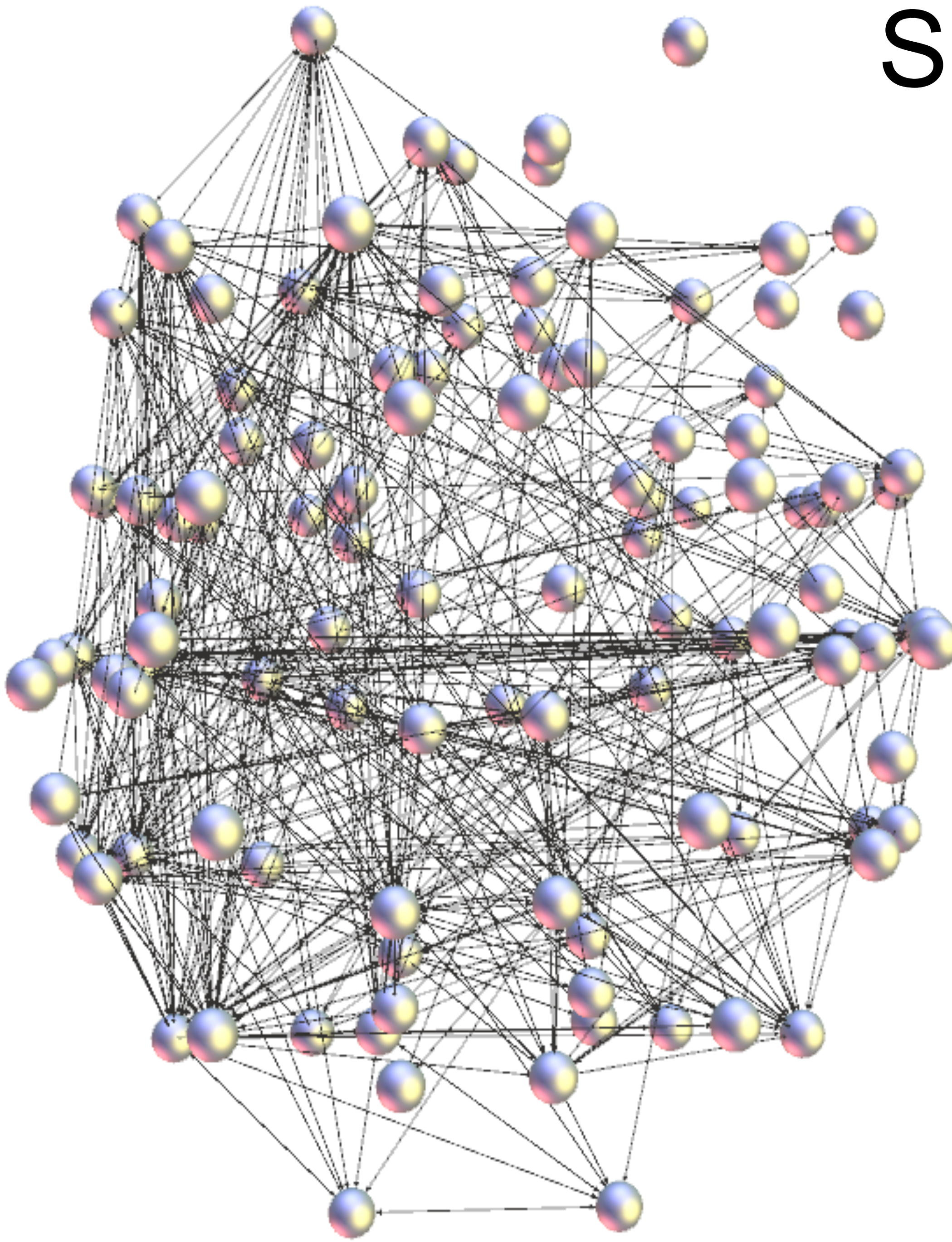

Atlanta (ATL)
Montgomery (MGM)
Columbus (CSG)
Albany (ABY)
Dothan (DHN)
Tallahassee (TLH)
Valparaiso (VPS)
Panama City (PFN)
Meridian (MEI)
Laurel/Hattiesburg (PIB)
Gulfport/Biloxi (GPT)
Baton Rouge (BTR)
New Orleans (MSY)
Lafayette (LFT)
Jackson/Vicksburg (JAN)
Birmingham (BHM)
Columbus (GTR)
Myrtle Beach (MYR)
Wilmington (ILM)
Jacksonville/Camp Lejeune (OAJ)
Hilton Head (HHH)
Jacksonville (JAX)
Gainesville (GNV)
St. Augustine (UST)
Daytona Beach (DAB)
New Smyrna Beach (DQN)
Sanford (SFB)
Orlando (MCO)
Tampa (TPA)
St. Petersburg (PIE)
Melbourne (MLB)
Sarasota/Bradenton (SRQ)
Ft. Myers (RSW)
Naples (APF)
Fort Lauderdale (FLL)
Miami (MIA)
Image © 2008 TerraMetrics
Image NASA
©2007 Google™



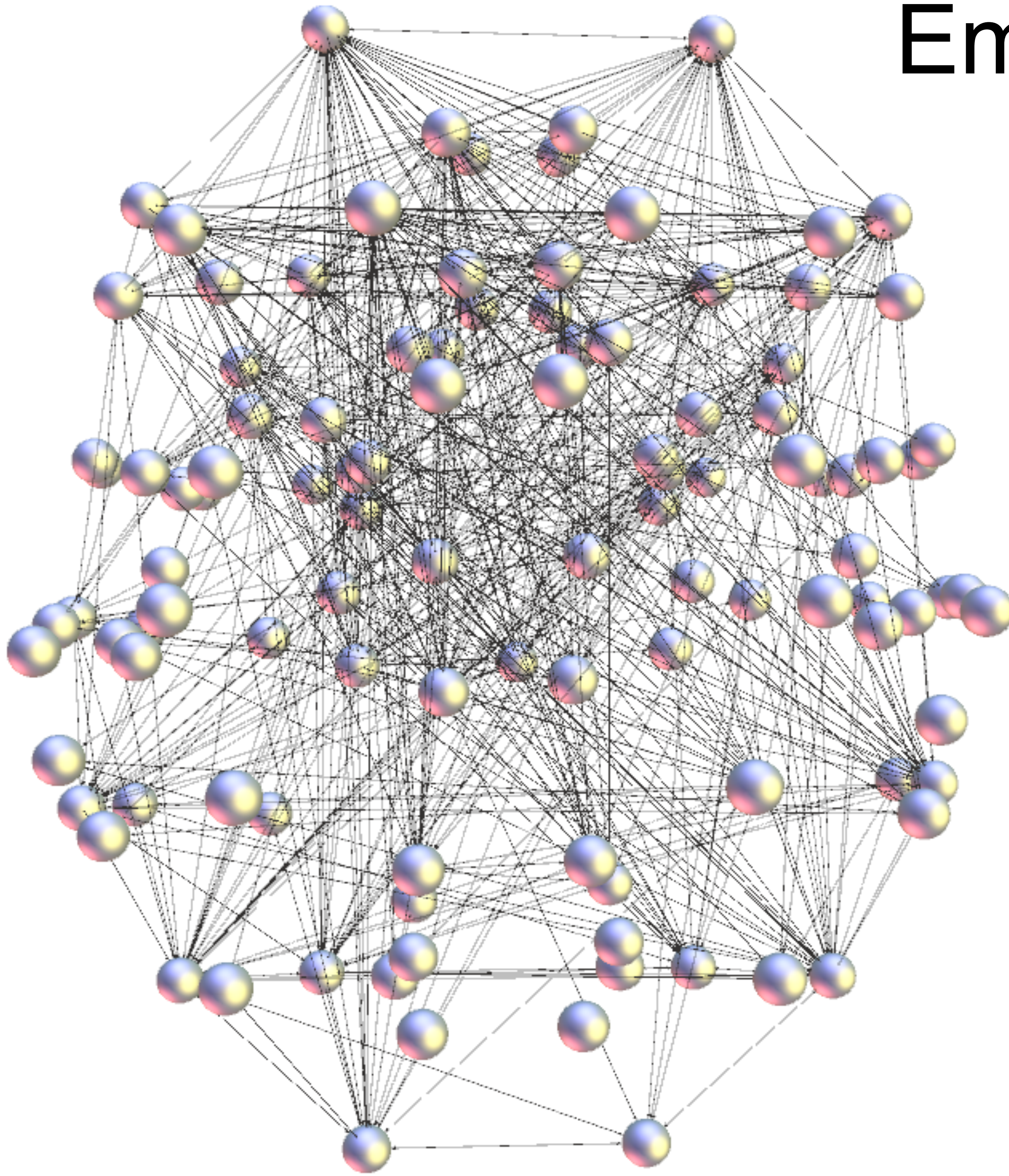
Hilary
Jennifer
Ilene
Leisha
dusty
katherine
laura r


Left Temporal Pole
Right Temporal Pole
Left Superior Parietal Lobule
Right Superior Parietal Lobule

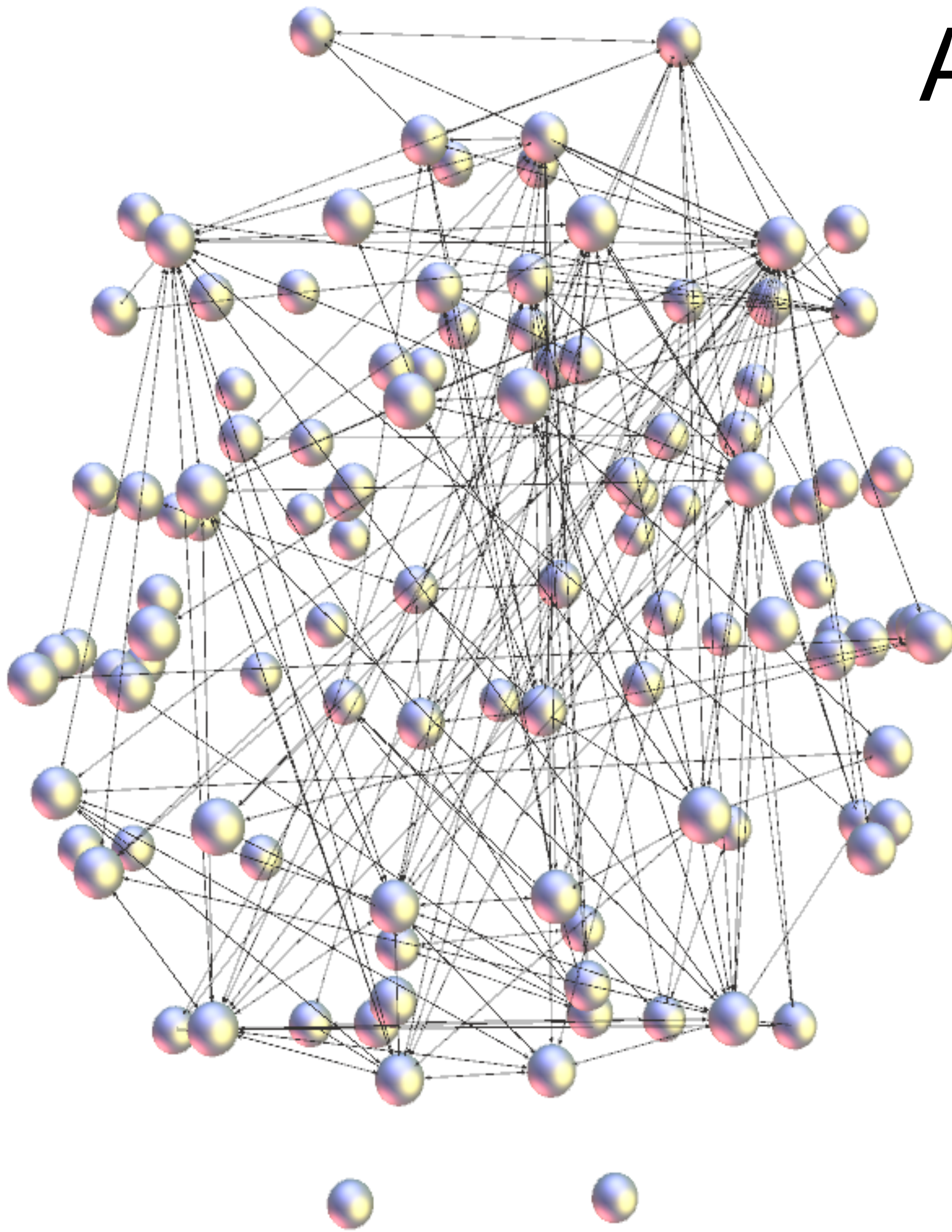
Semantics



Emotion



Attention



Comparing Domain Complexes

Can compare many things, for instance:

- Node overlap
  - Indicates local circuits shared by different domain complexes
- Edge overlap
  - Indicates functional connectivity/ cooperation shared by different domain complexes

Comparing Domain Complexes

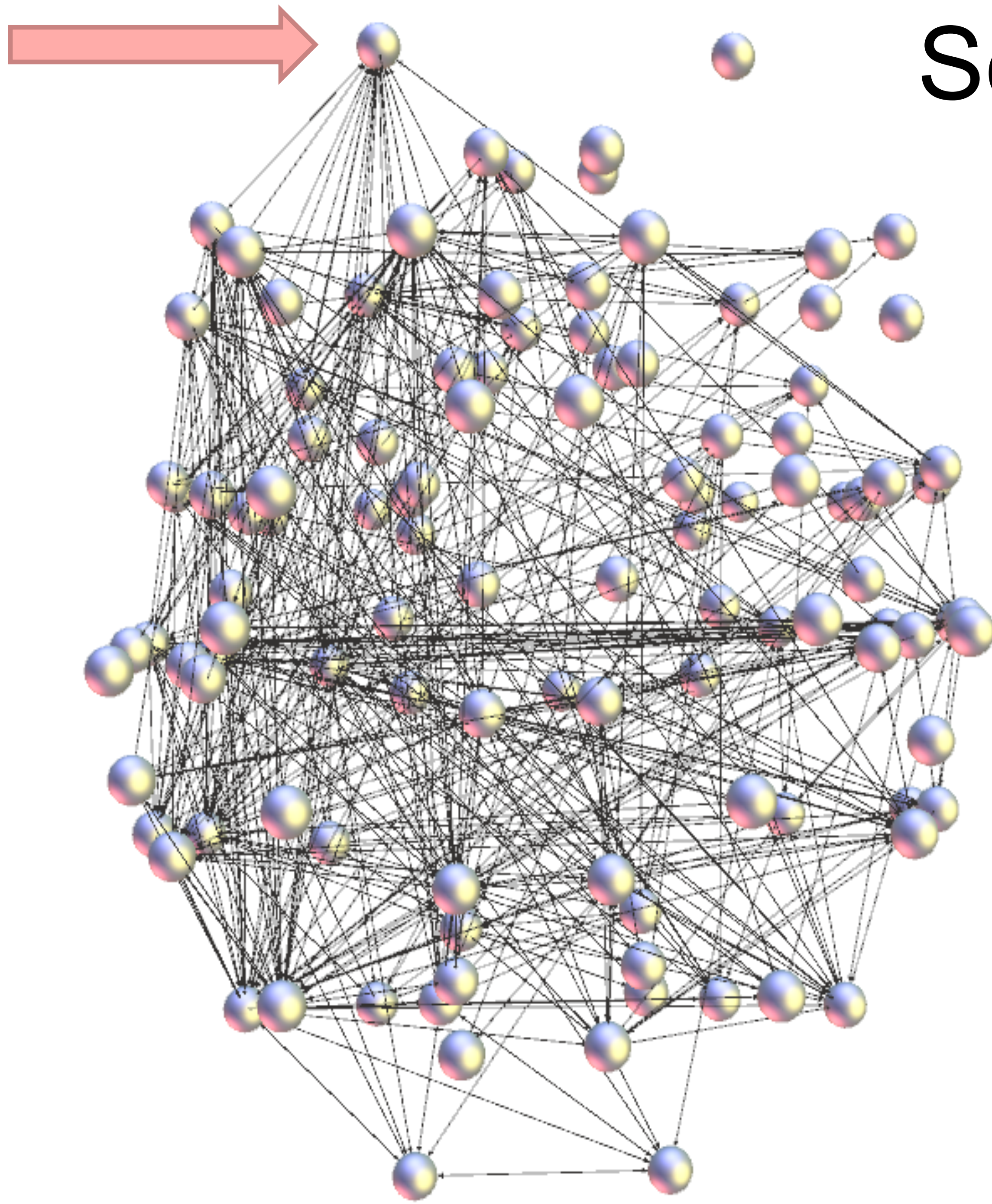
-Network topology

- May give clues about nature of function implementation

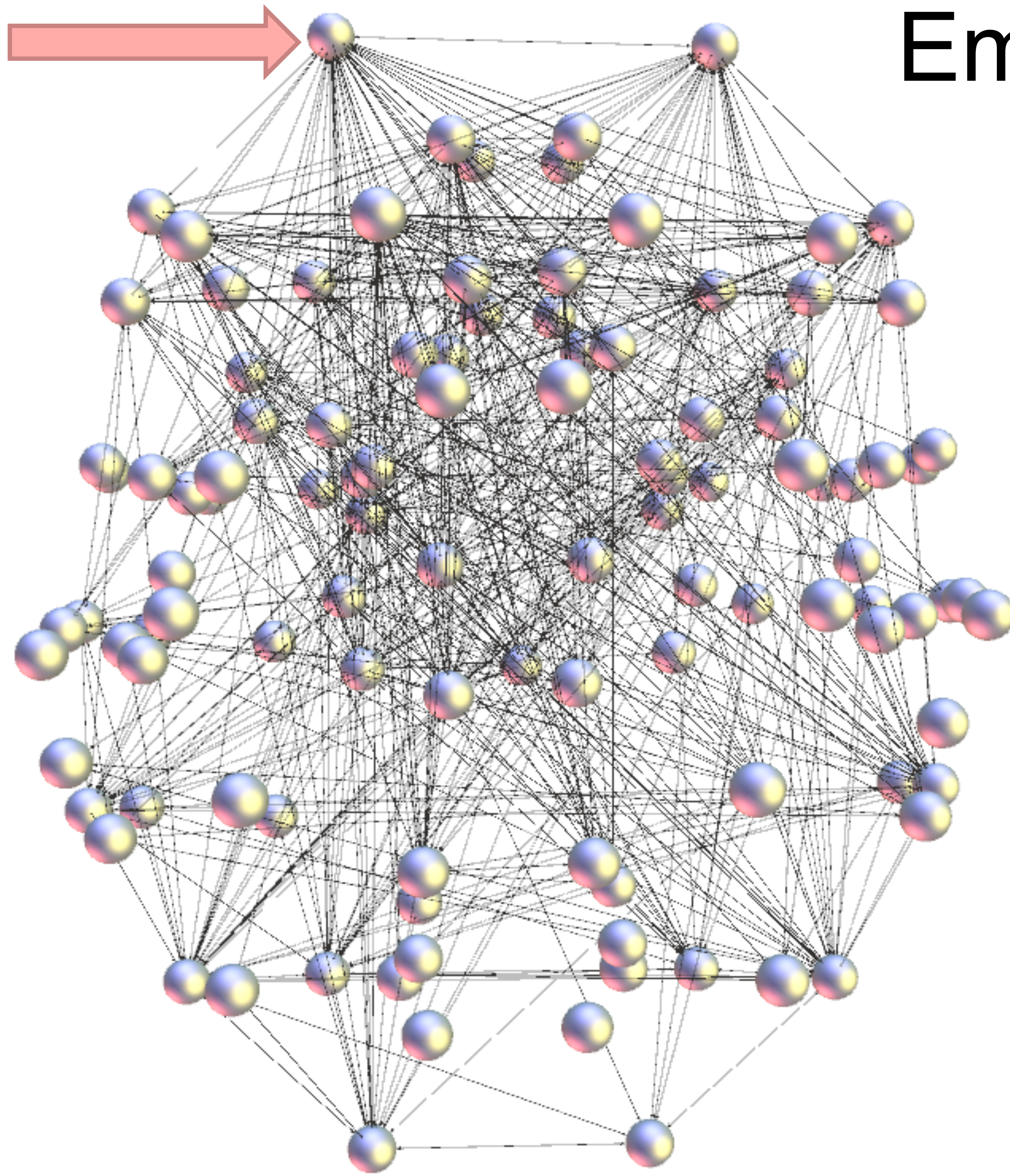
-Degree

- Indication of how many other regions a brain region typically cooperates with

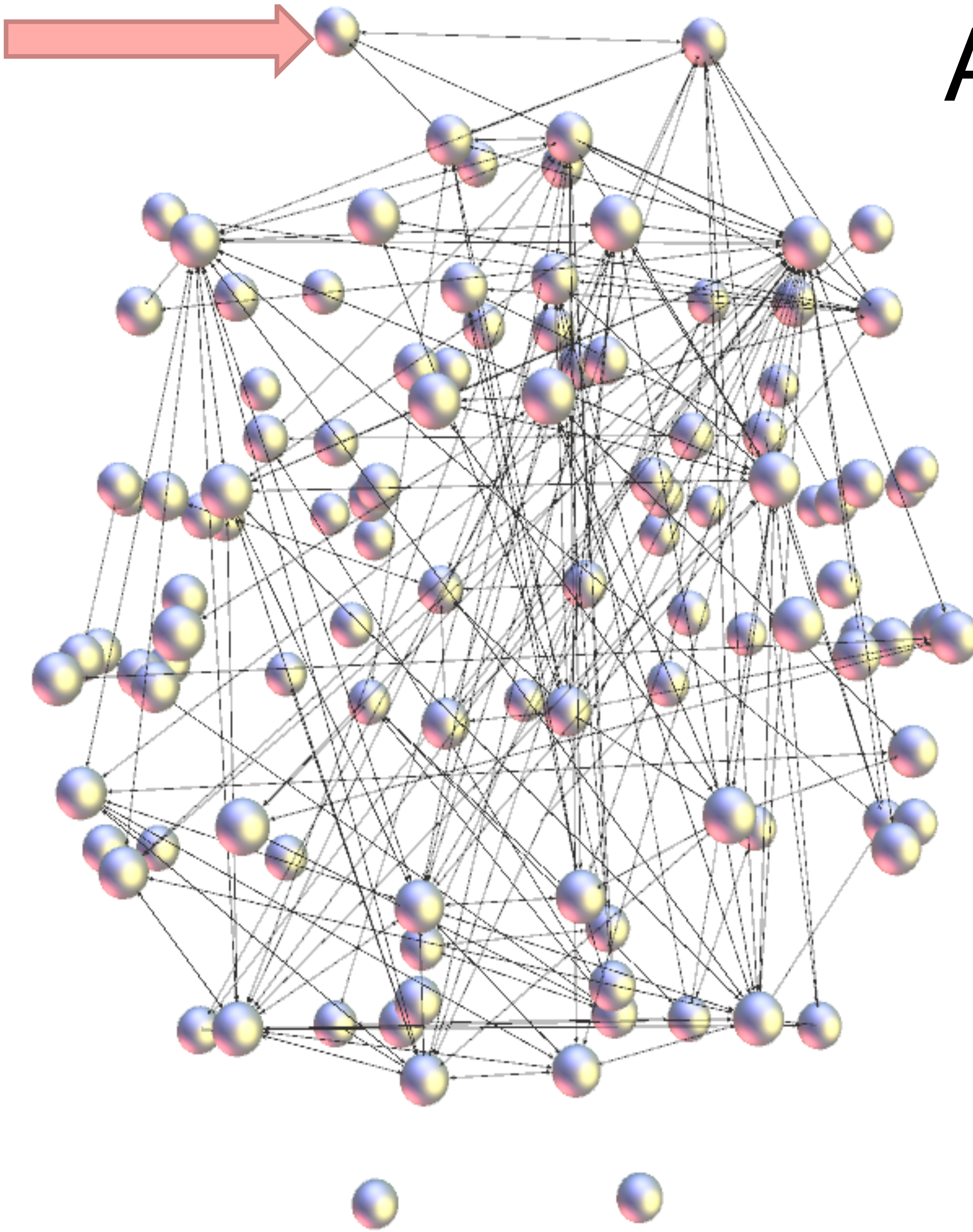
Semantics



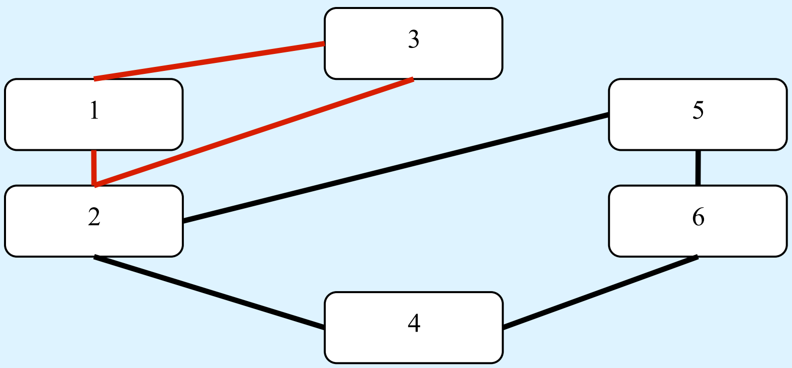
Emotion



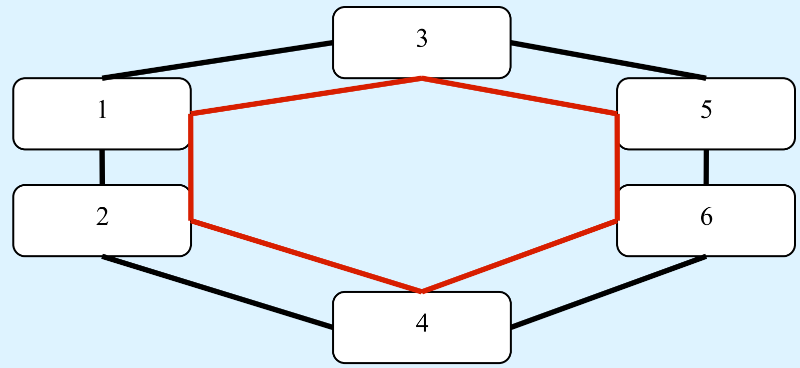
Attention



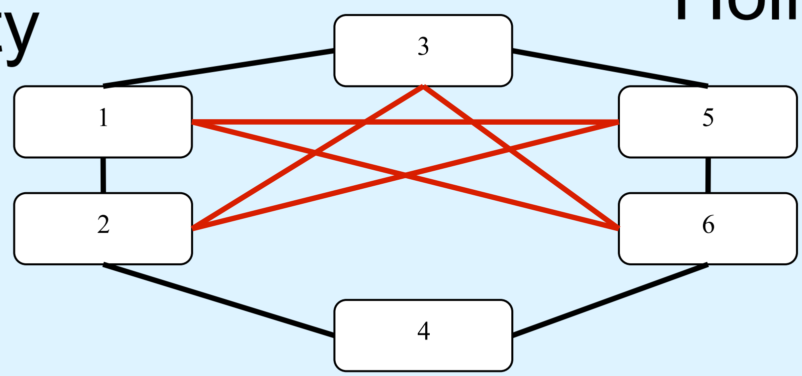
Overall functional architecture



Modularity



Holism / PDP



Reuse

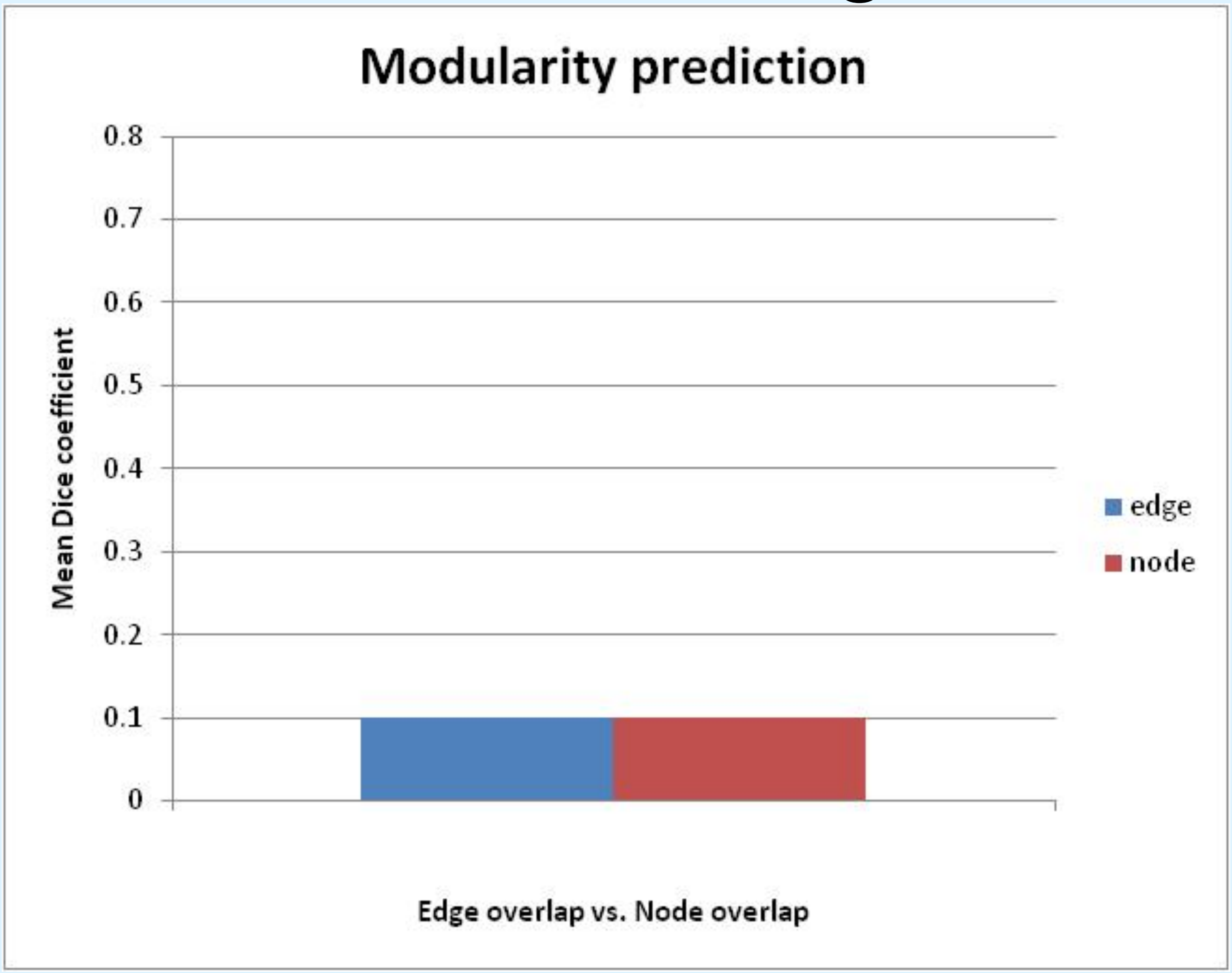
Node vs. Edge Overlap

Use Dice's coefficient: $2(o_{1,2})/(n_1+n_2)$

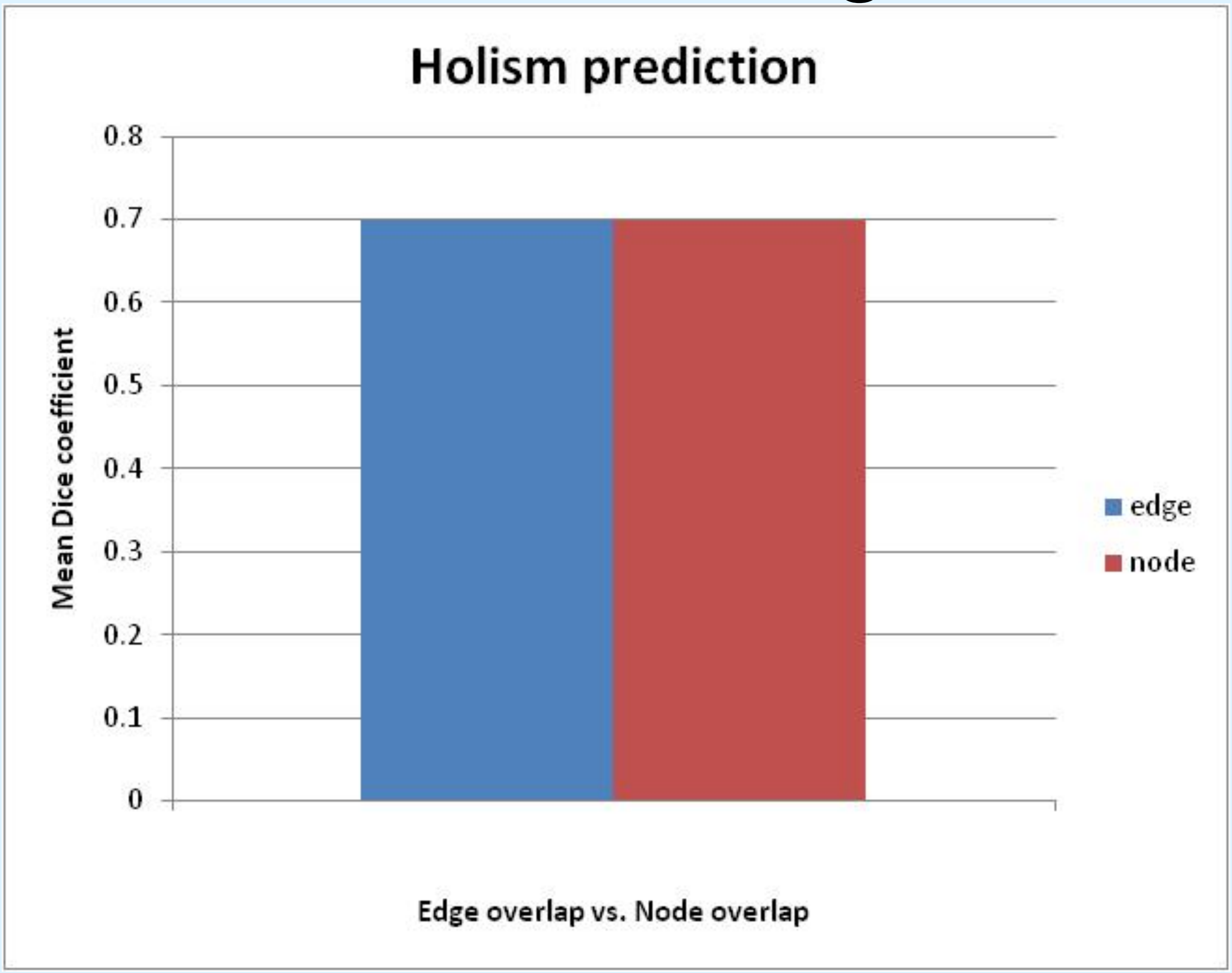
Predictions:

- Modularity: e, n
- Holism: E, N
- Reuse: e, N

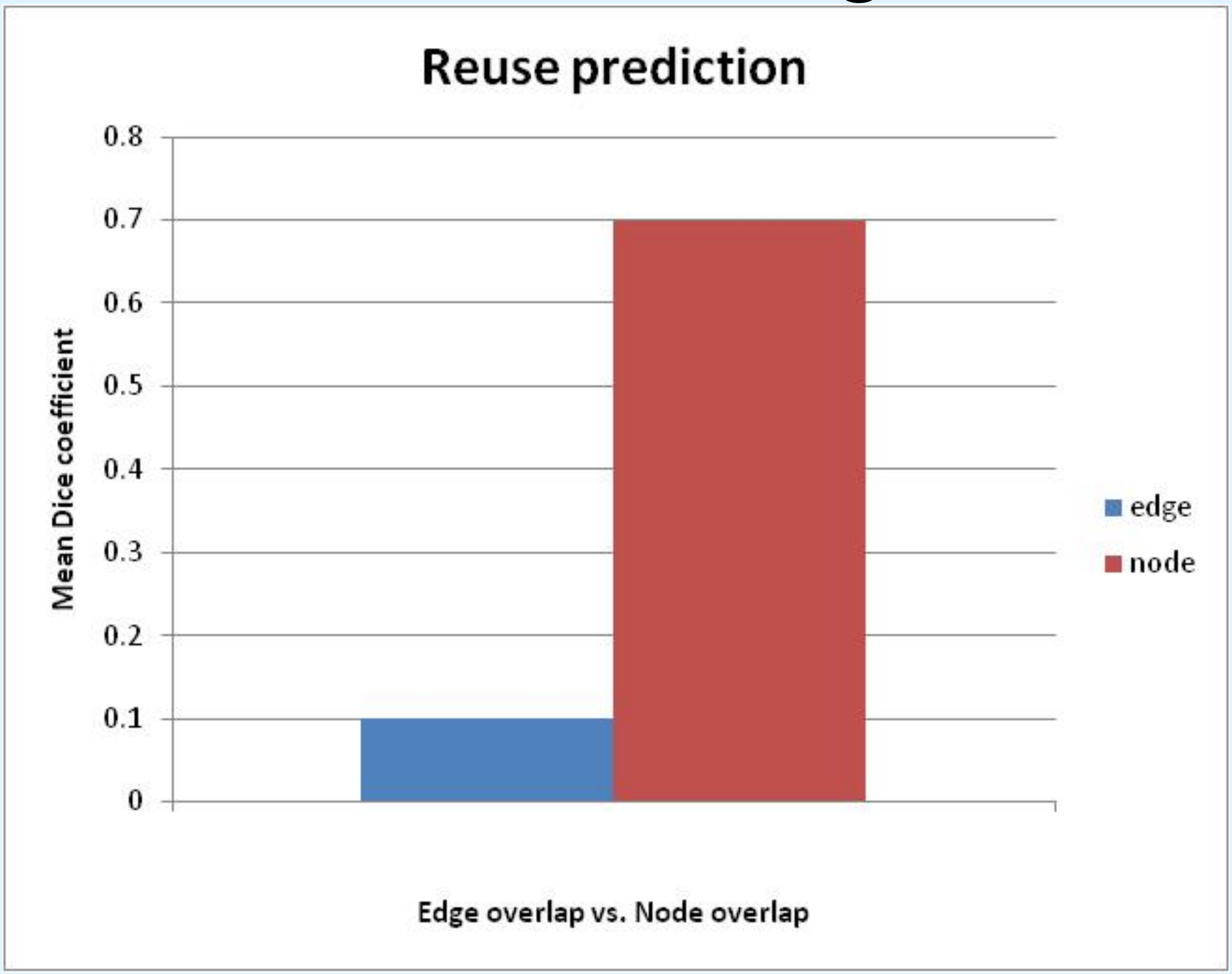
Nodes vs. Edges



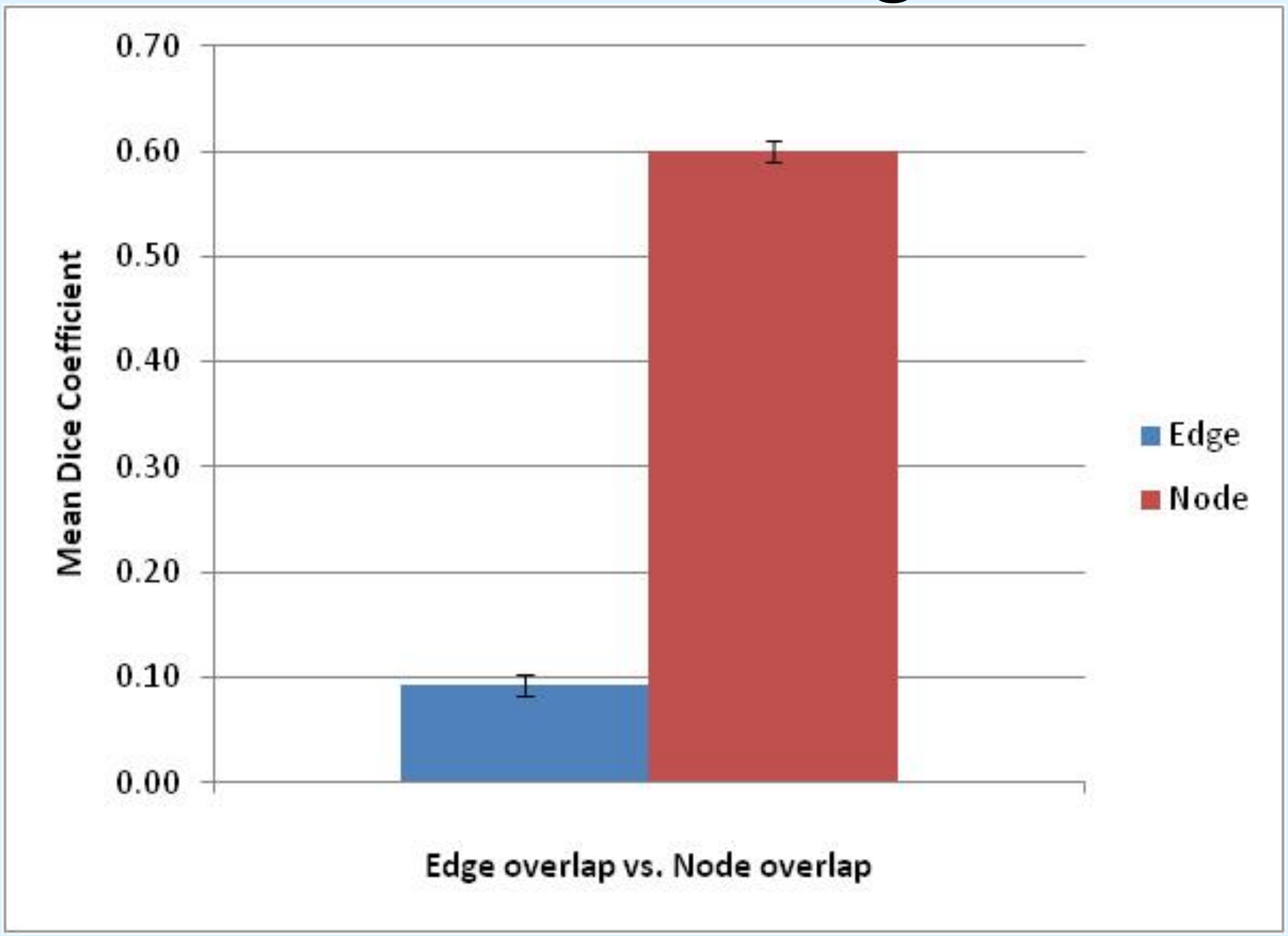
Nodes vs. Edges



Nodes vs. Edges



Nodes vs. Edges

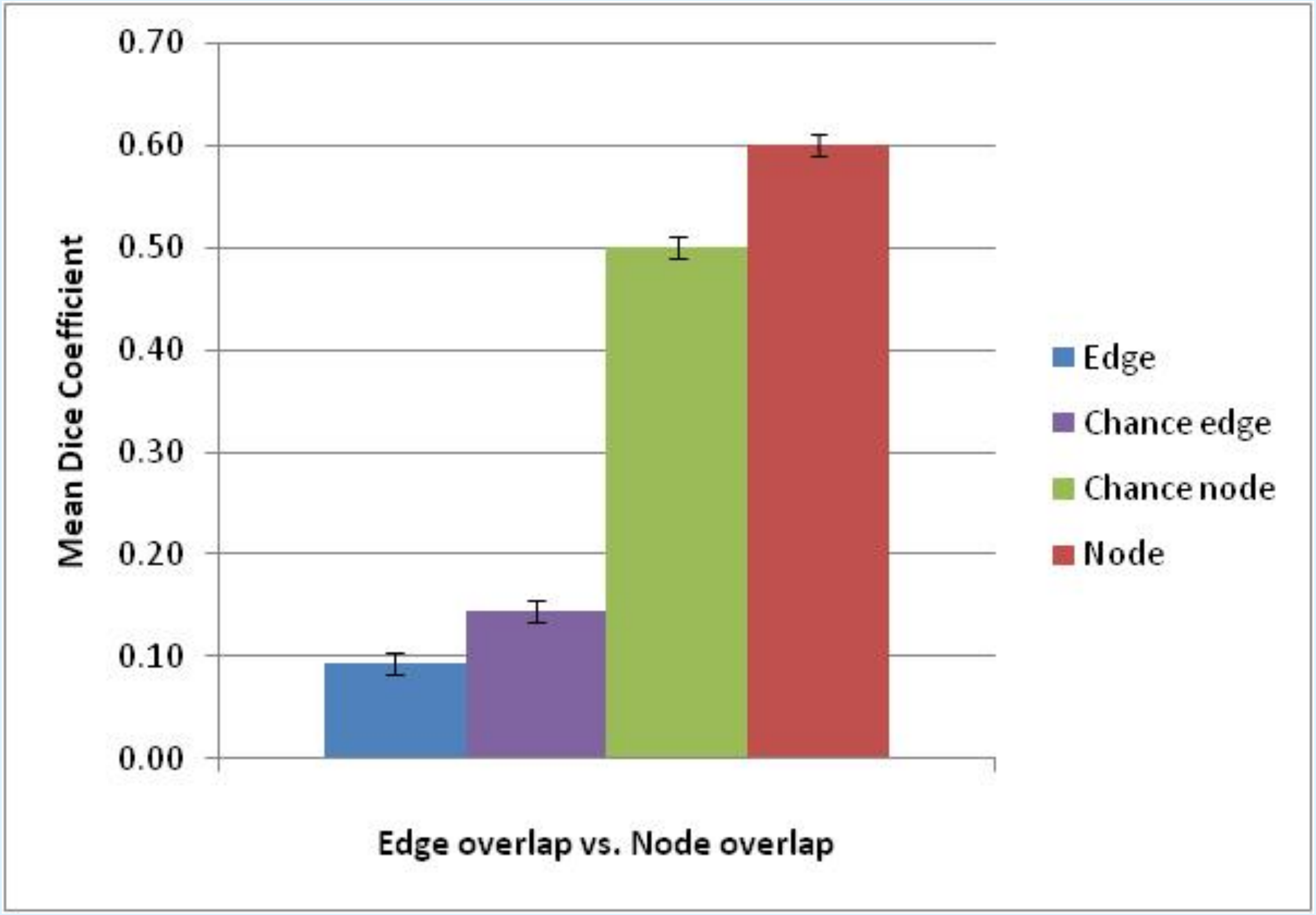


$p \ll 0.001$

But . . .

Maybe this result is just an artifact

- Given a small number of nodes (111)
- Large number of possible edges (6105)
- Get high node overlap and low edge overlap just by chance



0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Mean Dice Coefficient
Edge
Chance edge
Chance node
Node
Edge overlap vs. Node overlap

$p \ll 0.001$

Neural reuse

✓ I. Local circuits are typically redeployed in support of multiple cognitive functions across traditional task-domain boundaries

II. Redeployed circuits have the same “working” in each of the functional complexes they support

✓ III. Task domains will be differentiated at the network level

IV. More recent cognitive functions will utilize more, and more widely scattered local circuits

Neural reuse

I. Local circuits are typically redeployed in support of multiple cognitive functions across traditional task-domain boundaries

II. Redeployed circuits have the same “working” in each of the functional complexes they support

III. Task domains will be differentiated at the network level

IV. More recent cognitive functions will utilize more, and more widely scattered local circuits

Neural reuse

I. Local circuits are typically redeployed in support of multiple cognitive functions across traditional task-domain boundaries

II. Redeployed circuits have the same “working” in each of the functional complexes they support

III. Task domains will be differentiated at the network level

IV. More recent cognitive functions will utilize more, and more widely scattered local circuits

Neural reuse

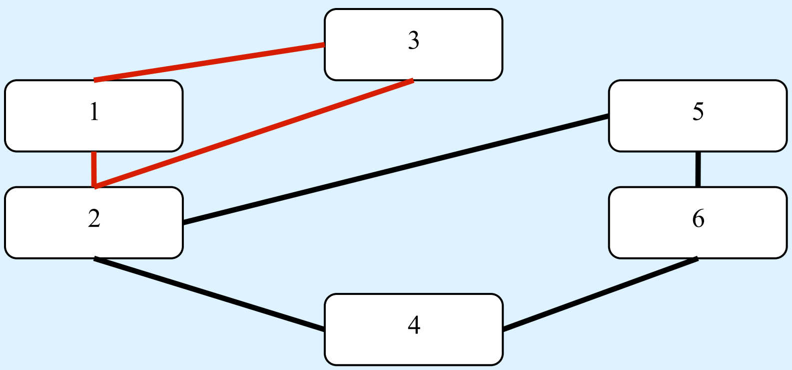
✓ I. Local circuits are typically redeployed in support of multiple cognitive functions across traditional task-domain boundaries

II. Redeployed circuits have the same “working” in each of the functional complexes they support

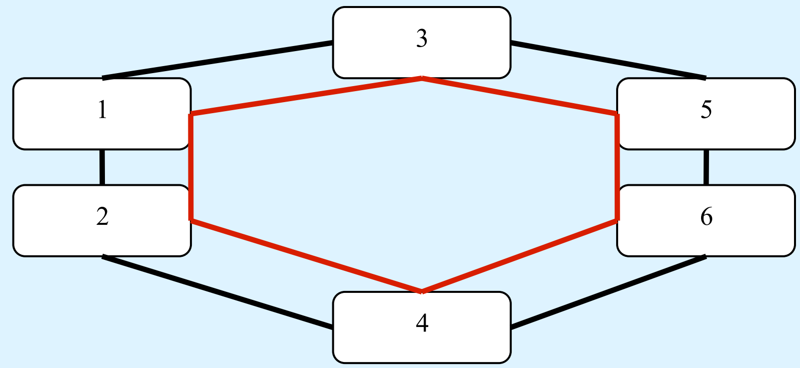
✓ III. Task domains will be differentiated at the network level

✓ IV. More recent cognitive functions will utilize more, and more widely scattered local circuits

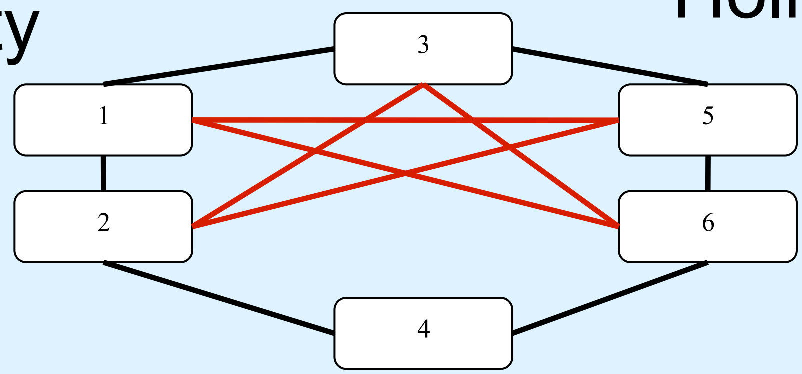
Overall functional architecture



Modularity



Holism / PDP



Reuse

Some implications

No use selectivity means **NO REVERSE INFERENCE, PLEASE**

Some implications

Regions of the brain should have differential, but measurable ***burden***.

This is perhaps correlated with diversity?

Some implications

Assigning computational/cognitive "workings" to local circuits will require cross-domain modeling

But is it ***Homology***?

Dagher et al. 1999: the reuse of motor circuits for

- action sequence planning
- abstract planning

This could be a serial homology, with shared developmental precursor, and “special qualities”

But is it ***Homology***?

Although, note there is no need for any "copying" of the shared structure

The selection pressure can operate on the ***networks***, which differ

But is it ***Homology***?

On the other hand,

Since what differentiates the two is precisely the ***different connections*** of the shared structure,

Is this a ***bone***, or a ***turtle shell***?

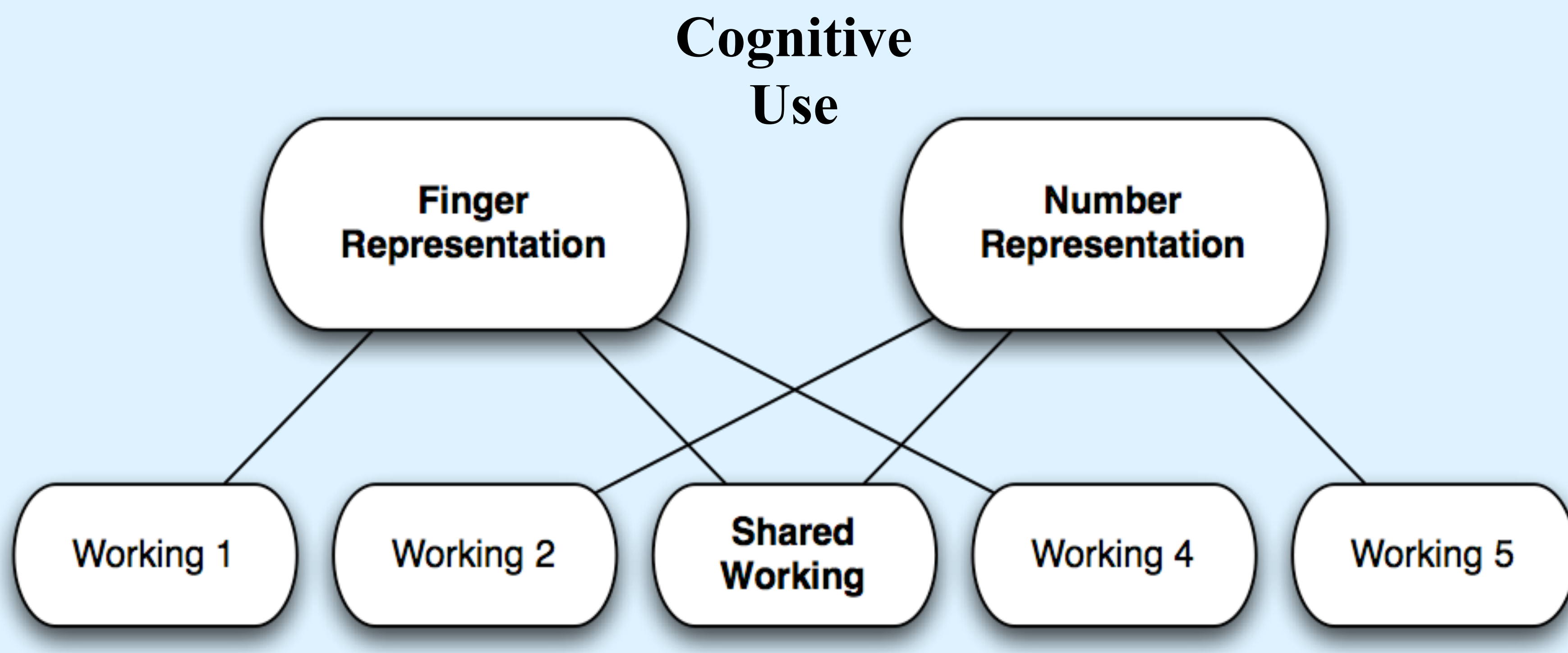
Finger gnosia and math

•***Finger gnosia*** is the ability to distinguish, in the absence of visual feedback, which fingers have been lightly touched.

•Developmentally, finger gnosia has been found to predict mathematical ability

	Digit Recognition	**Next Number**	**Place Value**	**Numeration**	**Calculation**
Finger Gnosia	.19*	.22**	.18*	.28**	.19*

Finger gnosia and math



But is it ***Homology***?

In this case the shared working appears to be a particular sort of storage resource: an array of pointers

Here any inheritance of functional character is much less clear; it is simply reuse of an available storage system

But is it ***Homology***?

And, of course, here again, differential function is achieved precisely in terms of ***differential connections*** to other "organs"

But is it ***Homology***?

On the other hand,

It does appear that the systems *fail* in similar ways

Does that count as a special quality?

So is it ***Homology***?

(I don’t have a conclusion)

Thanks to

Kevin Gold, RIT

Catherine Havasi, MIT

Marcie Penner-Wilger, Franklin & Marshall College

Luiz Pessoa, Indiana University

Olaf Sporns, Indiana University

Terry Stewart, University of Waterloo

Lucina Uddin, Stanford University