Modelling Natural Intelligence

Tony Prescott
University of Sheffield
United Kingdom

The
University
Of
Sheffield.

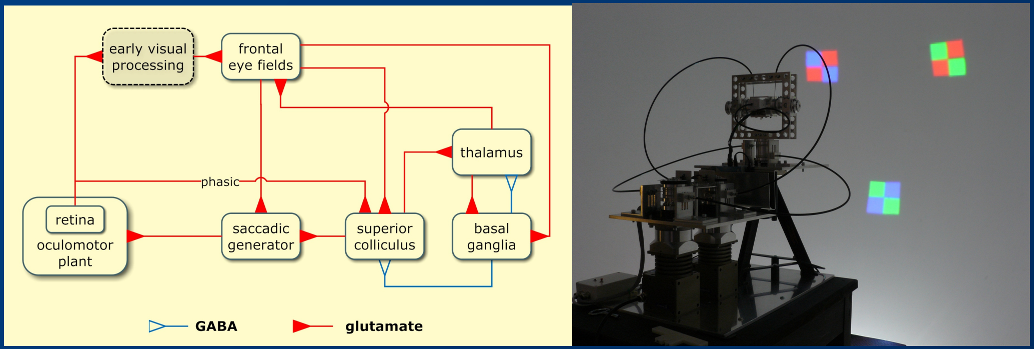
Research Strategy

Seek to understand the layered architecture of the brain by reverse-engineering, and emulating in robots, the sensori-motor loops underlying the control of eye movements in primates (including humans) and of vibrissal movements in rodents and other whiskered animals

ATL@S
Active Touch Laboratory at Sheffield

brl
Bristol Robotics Laboratory

Active Touch Laboratory (leader: Tony Prescott)



Active Vision Laboratory (leader: Kevin Gurney)

The problem of brain architecture

Behavioural integration:

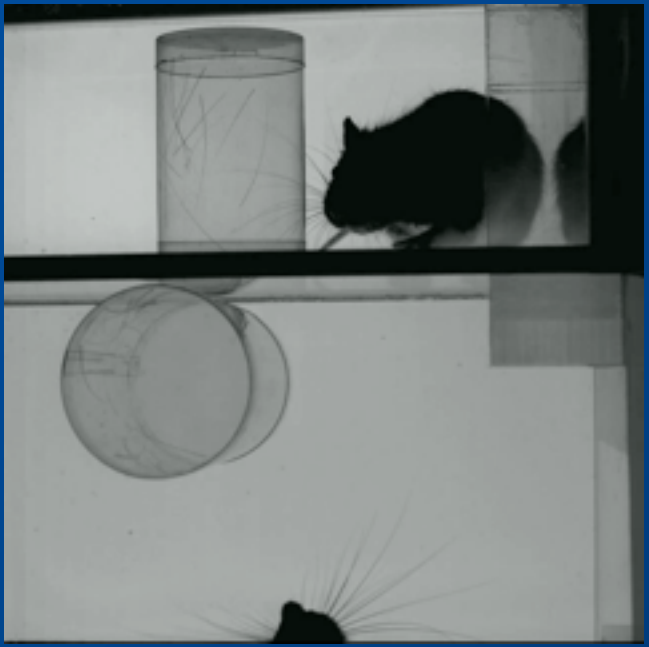
“the phenomenon so very characteristic of living organisms, and so very difficult to analyze: the fact that they behave as wholes rather than as the sum of their constituent parts. Their behavior shows integration, […] a process unifying the actions of an organism into patterns that involve the whole individual.”

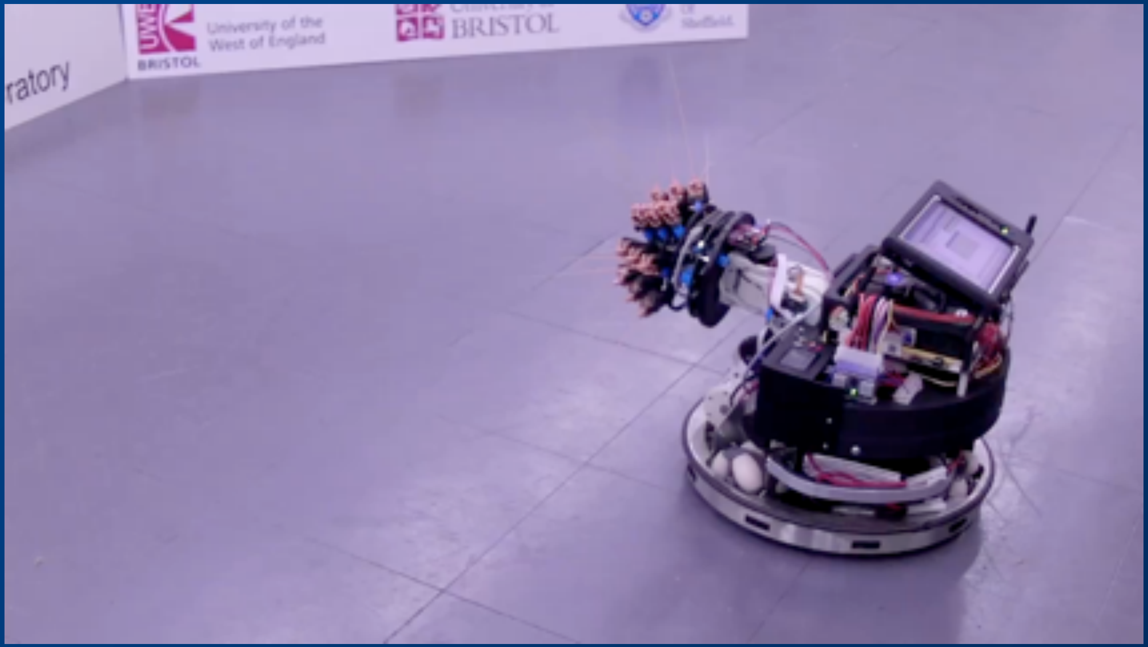
Ernest Barrington, 1967

Action selection: the task of resolving conflicts between competing behavioral alternatives

(Also known as ‘response selection’, ‘decision making’, ‘behavioral choice’, ‘motor program selection’)

Investigating brain architecture through active touch sensing in animals and robots

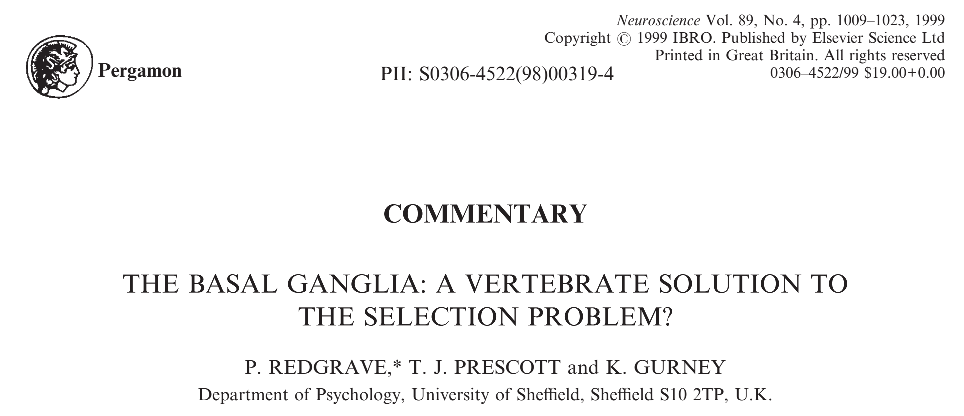




Adaptive Behavior 1999, 7(1), 99-127

Layered Control Architectures in Robots and Vertebrates

TONY J. PRESCOTT, PETER REDGRAVE, AND KEVIN GURNEY
University of Sheffield, UK



Pergamon

Neuroscience Vol. 89, No. 4, pp. 1009–1023, 1999
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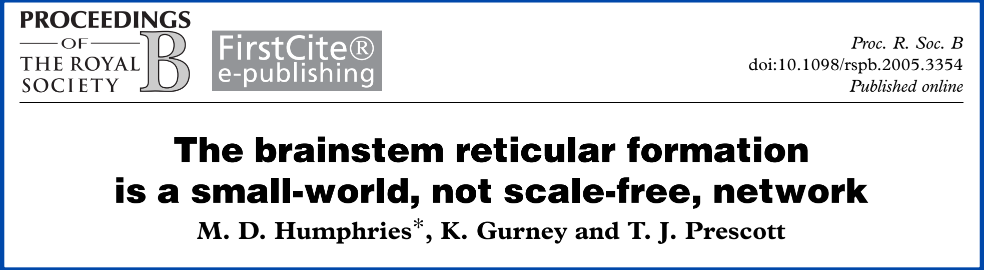
COMMENTARY

THE BASAL GANGLIA: A VERTEBRATE SOLUTION TO THE SELECTION PROBLEM?

P. REDGRAVE,* T. J. PRESCOTT and K. GURNEY
Department of Psychology, University of Sheffield, Sheffield S10 2TP, U.K.



PROCEEDINGS OF THE ROYAL SOCIETY B

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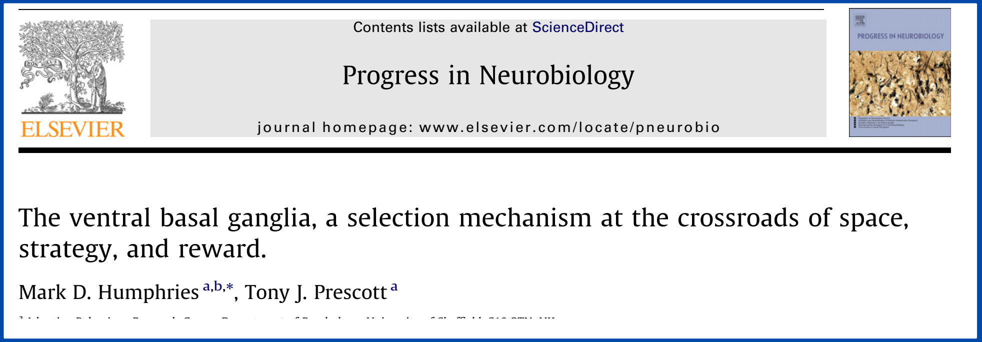
doi:10.1098/rspb.2005.3354
Published online

The brainstem reticular formation is a small-world, not scale-free, network

M. D. Humphries*, K. Gurney and T. J. Prescott



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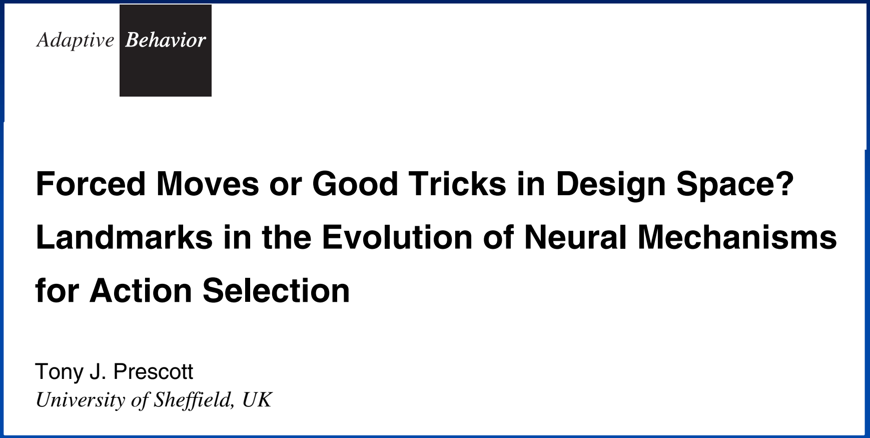
PROGRESS IN NEUROBIOLOGY

The ventral basal ganglia, a selection mechanism at the crossroads of space, strategy, and reward.

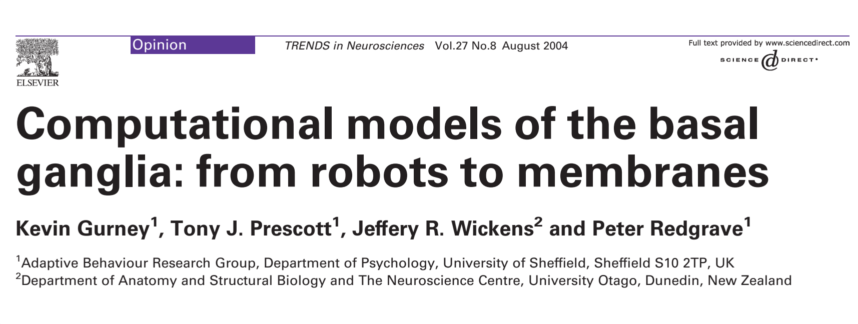
Mark D. Humphries [a,b,*], Tony J. Prescott [a]



Adaptive ***Behavior***

Forced Moves or Good Tricks in Design Space? Landmarks in the Evolution of Neural Mechanisms for Action Selection

Tony J. Prescott
University of Sheffield, UK



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Opinion

TRENDS in Neurosciences Vol.27 No.8 August 2004

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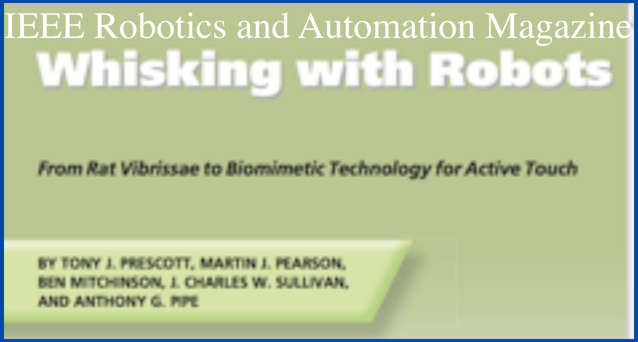
Computational models of the basal ganglia: from robots to membranes

Kevin Gurney[1], Tony J. Prescott[1], Jeffery R. Wickens[2] and Peter Redgrave[1]

[1]Adaptive Behaviour Research Group, Department of Psychology, University of Sheffield, Sheffield S10 2TP, UK
[2]Department of Anatomy and Structural Biology and The Neuroscience Centre, University Otago, Dunedin, New Zealand

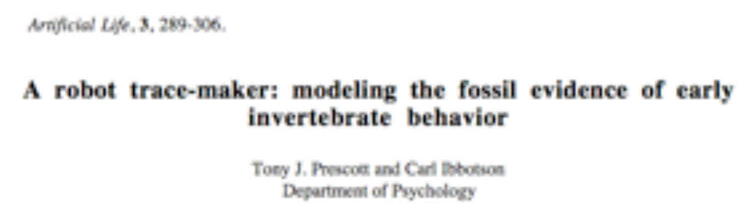


IEEE Robotics and Automation Magazine

Whisking with Robots

From Rat Vibrissae to Biomimetic Technology for Active Touch

BY TONY J. PRESCOTT, MARTIN J. PEARSON, BEN MITCHINSON, J. CHARLES W. SULLIVAN, AND ANTHONY G. PIPE



Artificial Life, **3**, 289-306.

A robot trace-maker: modeling the fossil evidence of early invertebrate behavior

Tony J. Prescott and Carl Ibbotson
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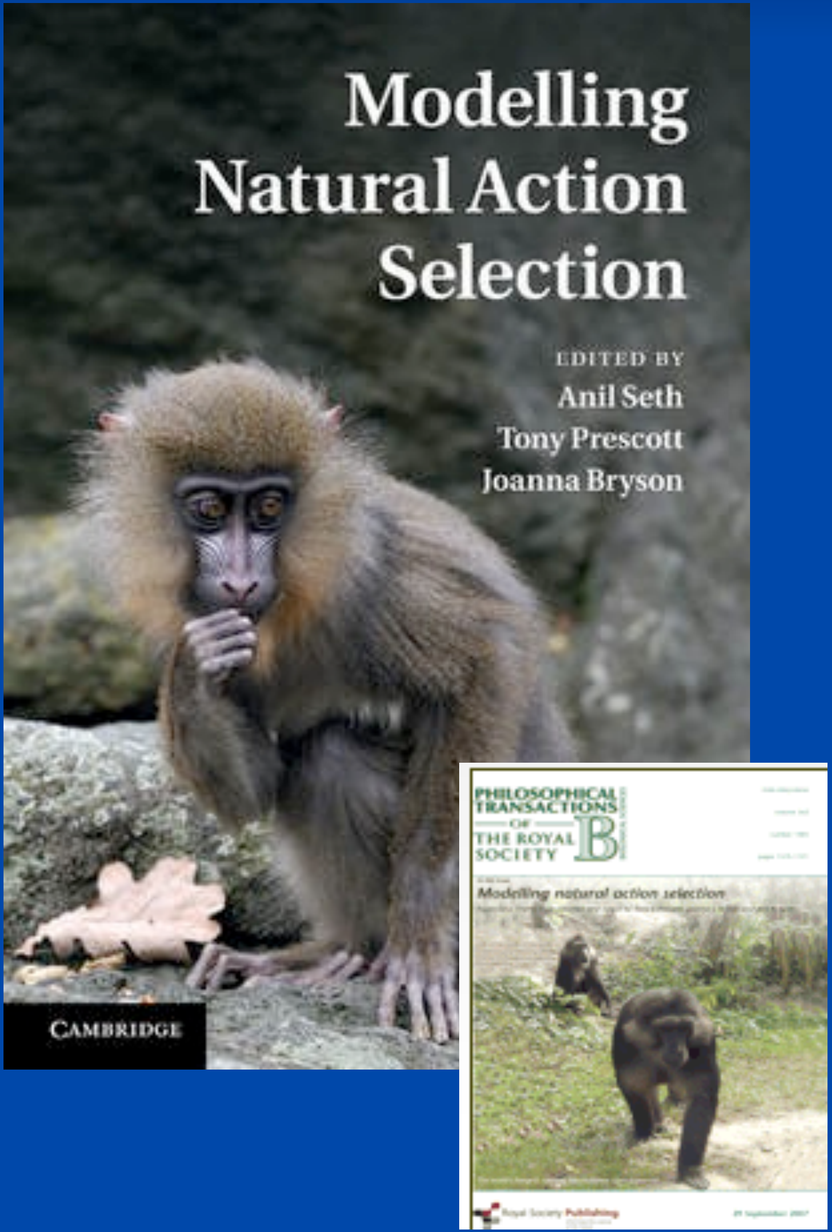

Modelling Natural Action Selection

EDITED BY
Anil Seth
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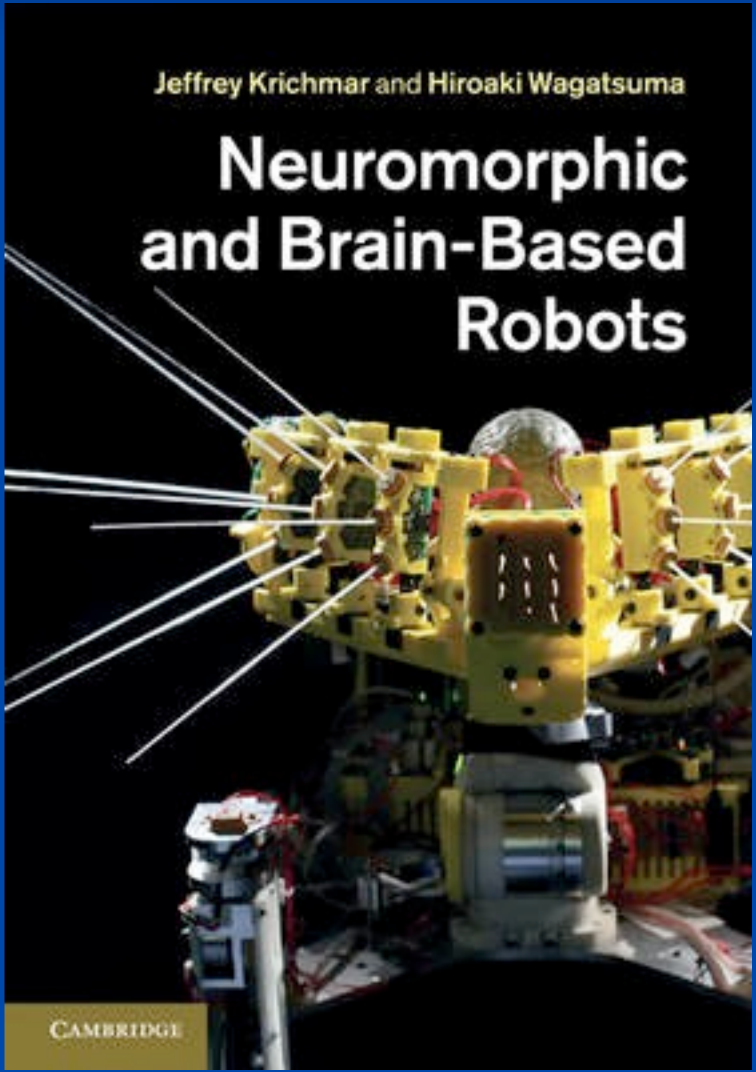
CAMBRIDGE

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Modelling natural action selection

Royal Society Publishing

29 September 2007



Jeffrey Krichmar and Hiroaki Wagatsuma

Neuromorphic and Brain-Based Robots

CAMBRIDGE

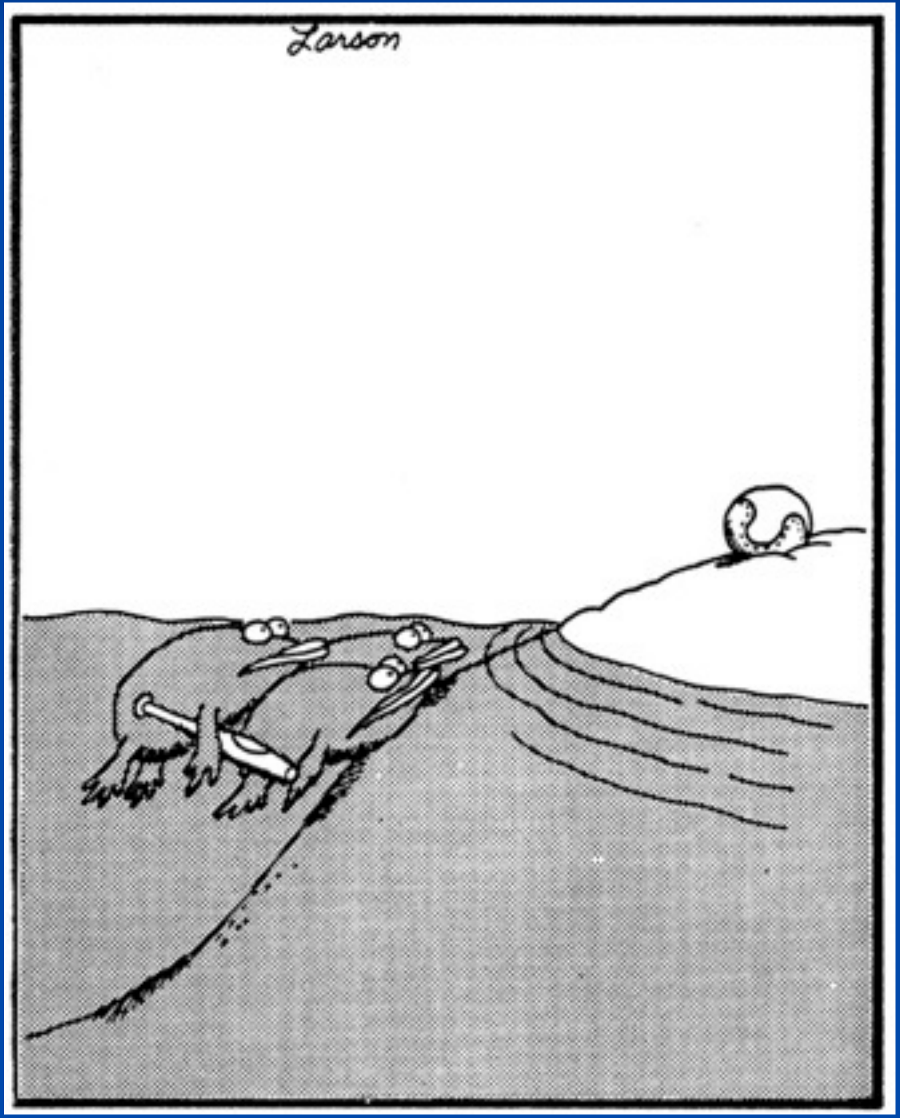
Modularity as Near Decomposability

"The frequencies of interaction among elements in any particular subsystem of a system are an order of magnitude or two greater than the frequencies of interaction between the subsystems. We call systems with this property nearly completely decomposable systems, or for short, nearly decomposable (ND) systems"

(Simon and Ando, 1961; Simon, 2002)

Great moments in evolution I

Jellyfish



Great moments in evolution

Sponges

(Porifera)

Cnidarians

(hydra, most jelly fish, anenomies)

Urbilaterians

Flatworms

Arthropods

Molluscs

Annelids

Nemerteans

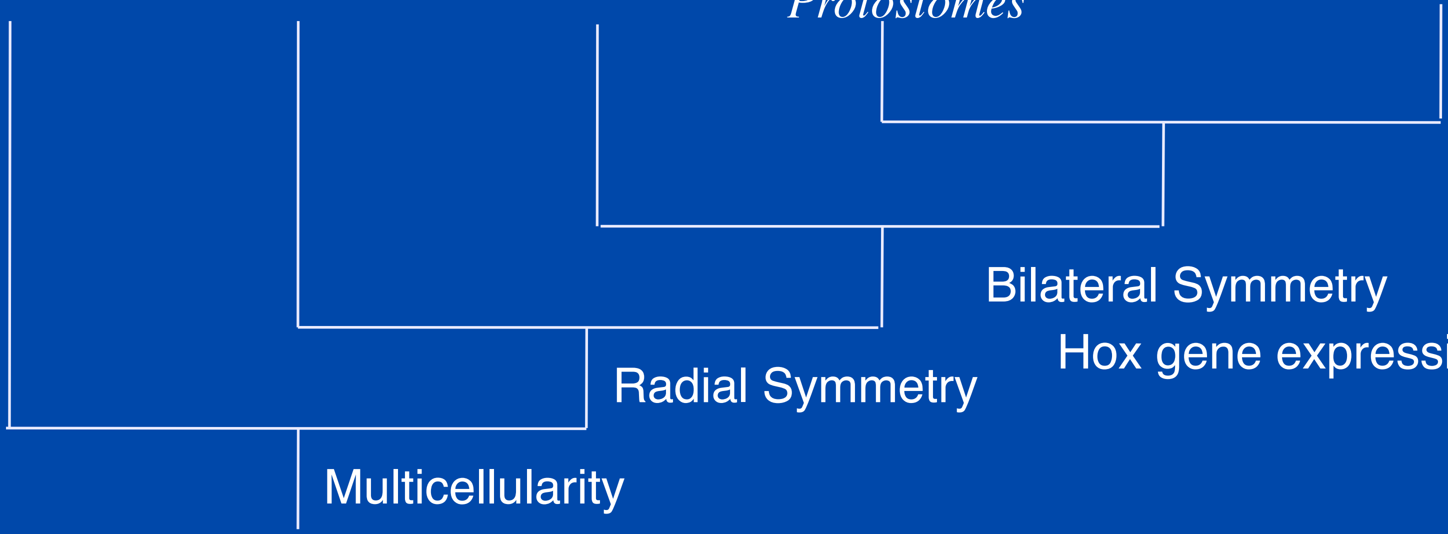
Protostomes

Chordates

Hemichordates

Echinoderms

Deuterostomes



Bilateral Symmetry

Hox gene expression

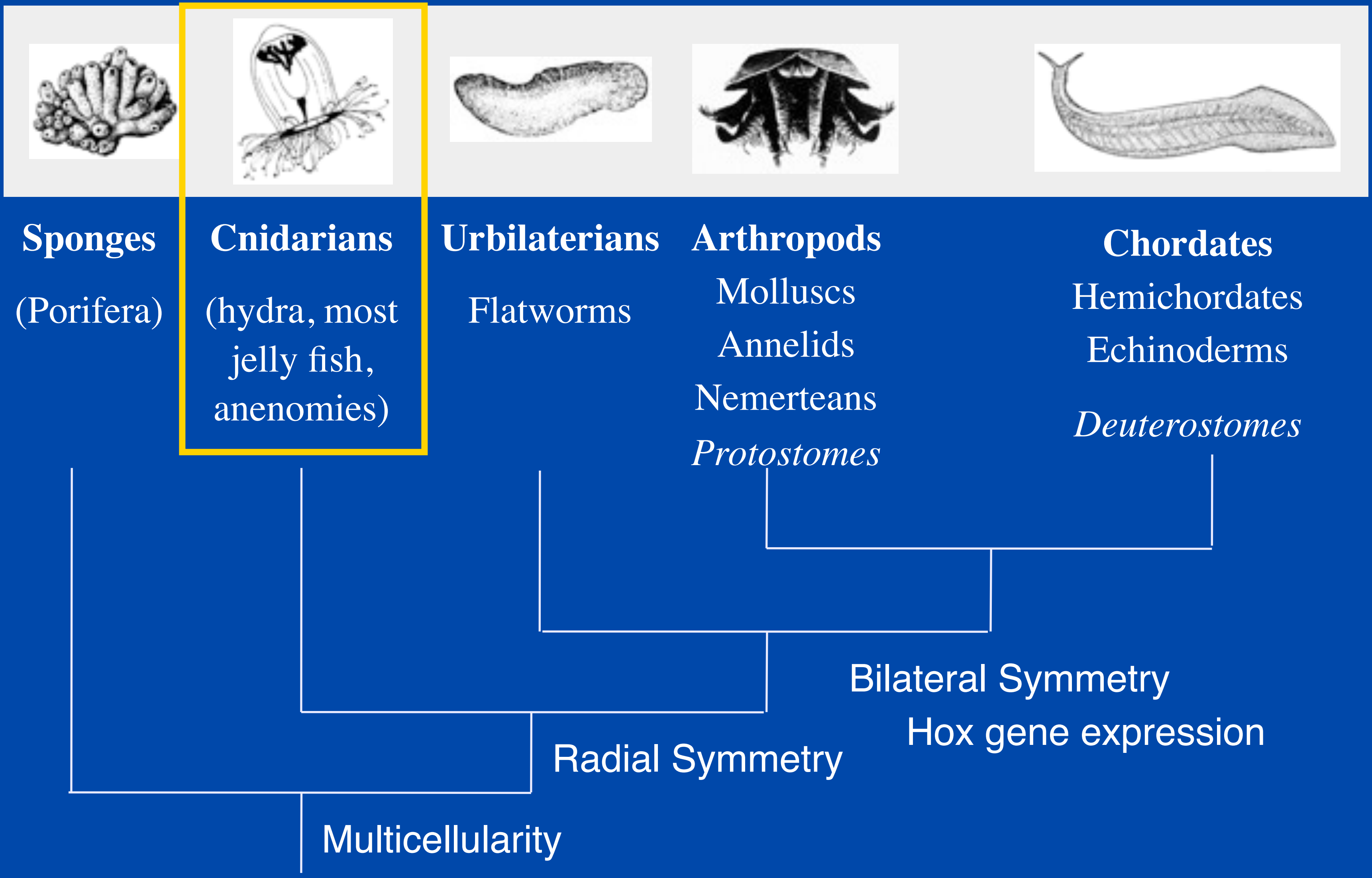
Radial Symmetry

Multicellularity

Metazoans

Adapted from Raff, 1996.

Great moments in evolution



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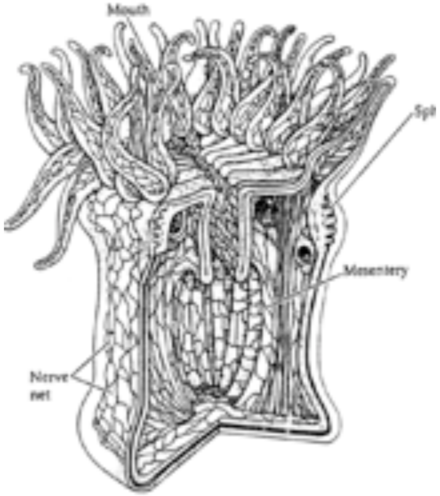
Nemaia Simplex: fossil jellyfish from the Vendian (Precambrian) period ~550+ myo

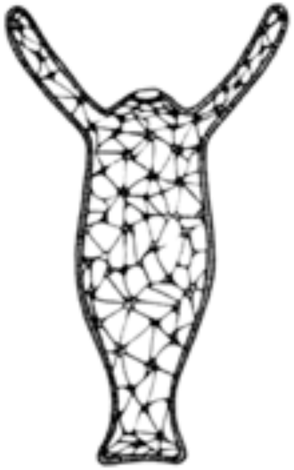
The first nervous systems (Cnidarians)

The nervous system consists of a nerve net (or multiple nerve nets). There are multi-cellular sense organs as well as some aggregations of nerve cells.

Jellyfish nerve net
(Bullock, 1977)



Sea Anenome
(Grimmelikhuijen, 1995)



Hydra (idealised)
(Marshall and Williams, 1972)

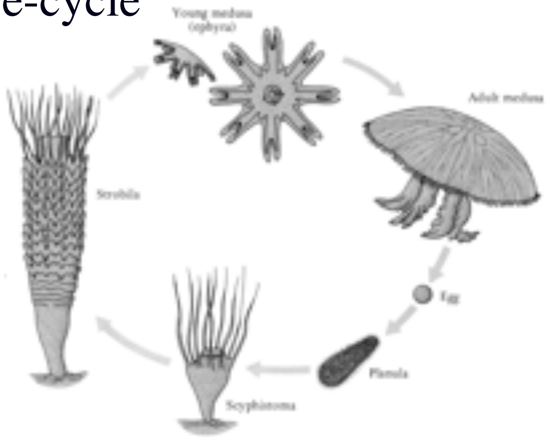
Hydra (actual)
(Grimmelikhuijen, 1995)

Aurelia aurita (scyphomedusa)

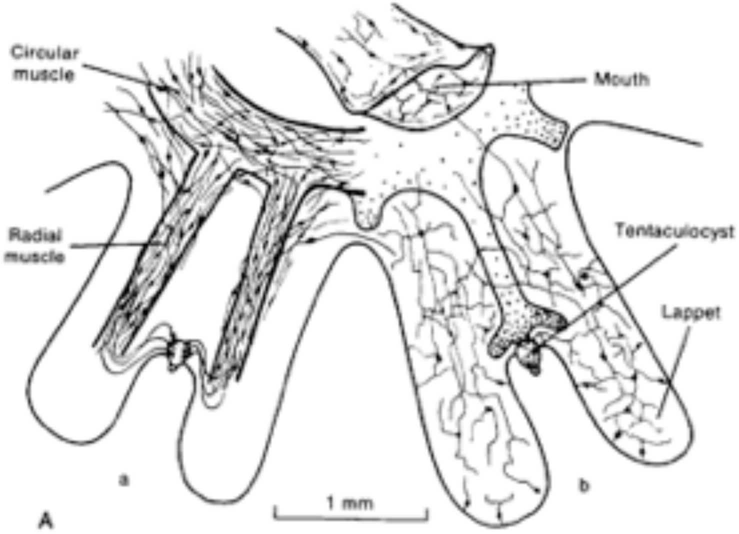
aka “Moon jelly”

Aurelia aurita: behavioural decomposition of control

Life-cycle



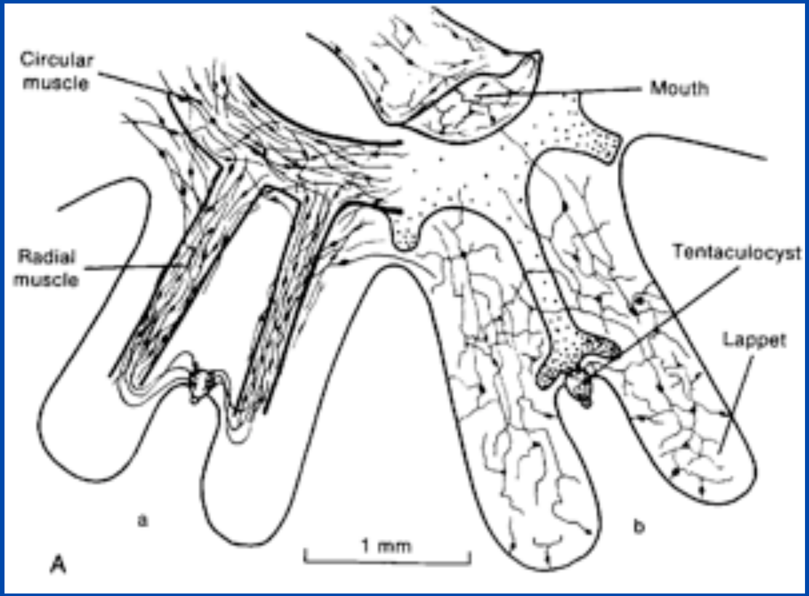
Feeding (left) and swimming (right) behaviours.

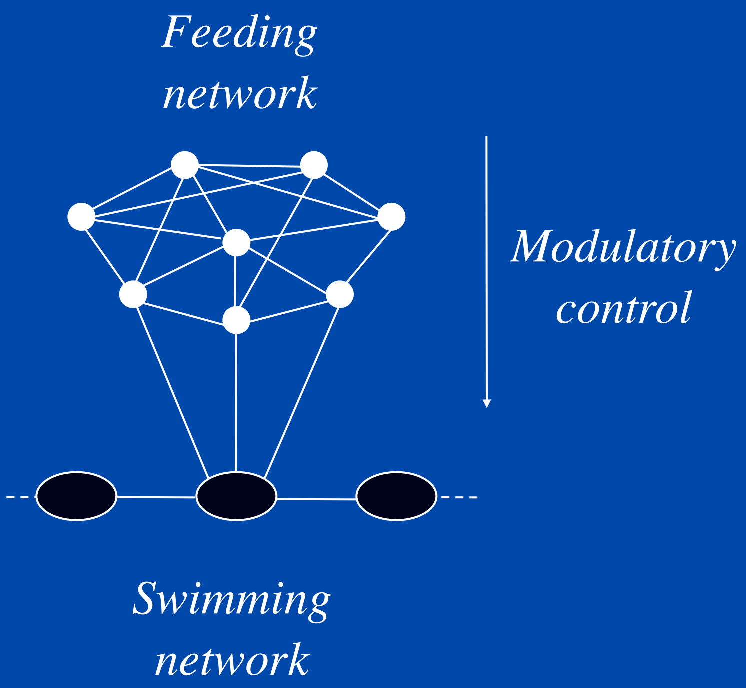


Two arms of the bell showing the main structures related to the two functionally distinct nerve nets for: (a) swimming (b) feeding.

From Horridge 1956

Aurelia aurita—layered architecture





Feeding network

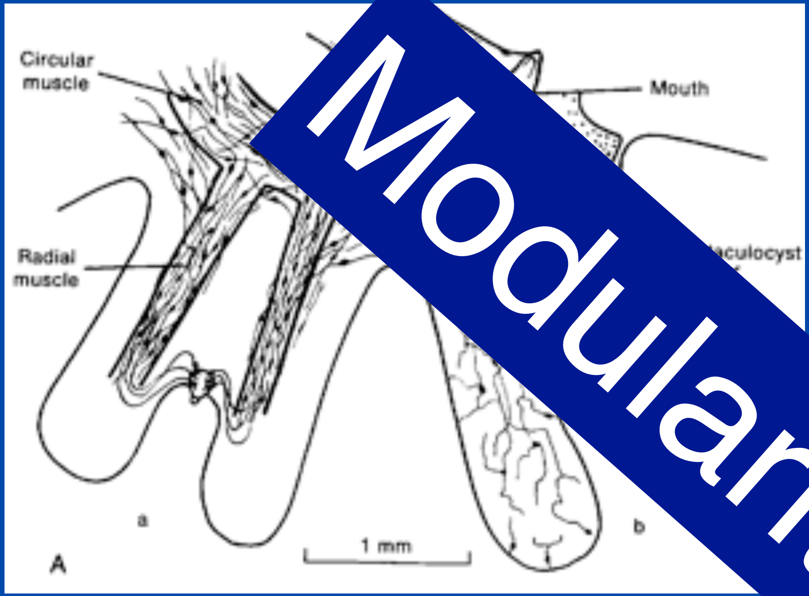
Modulatory control

Swimming network

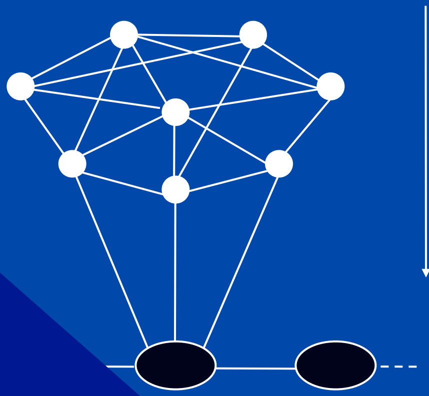
The two functionally distinct nerve nets make contact in neuron clusters termed **rhopalia** (or marginal ganglia), the swimming network appears to be under the modulatory control of the diffuse feeding network

Based on Horridge 1956

Aurelia aurita—layered architecture



Feeding network



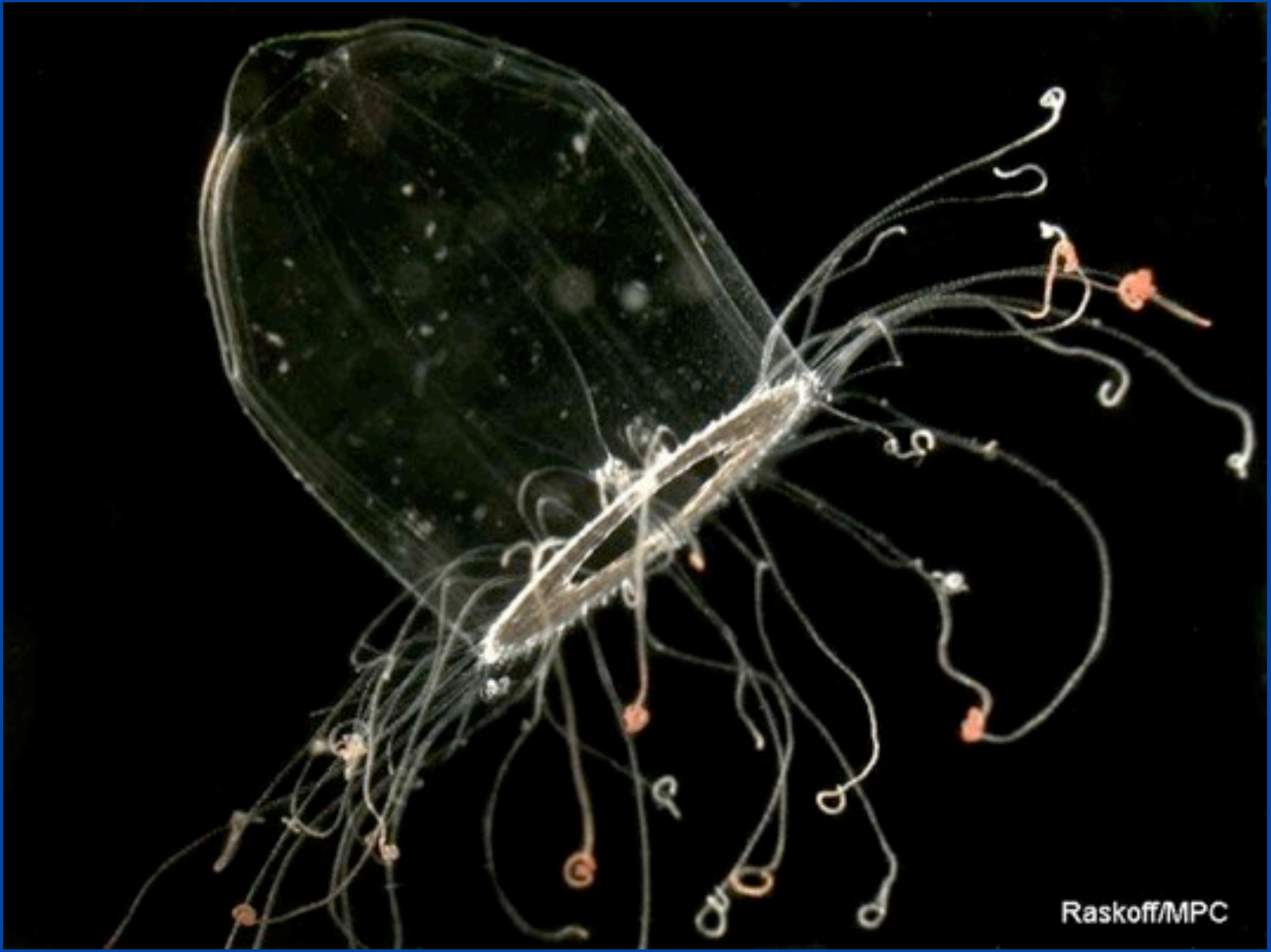
Modulatory control

[illegible]ing

The two functionally distinct nerve nets make [illegible] in neuron clusters termed **rhopalia** (or marginal ganglia), the swimming network appears to be under the modulatory control of the diffuse feeding network

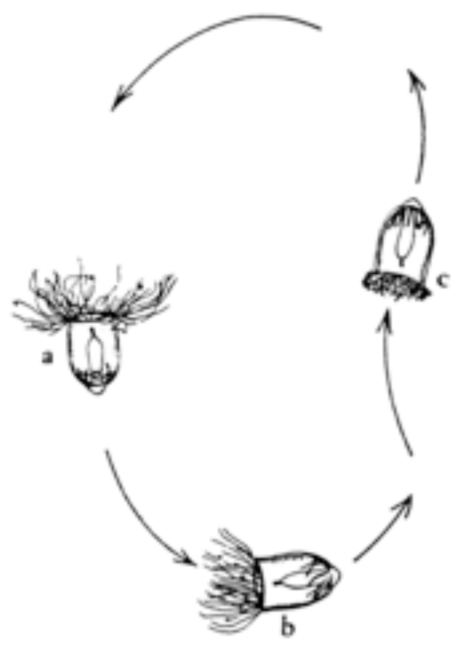
Based on Horridge 1956

Aglantha Digitale (hydromedusae)

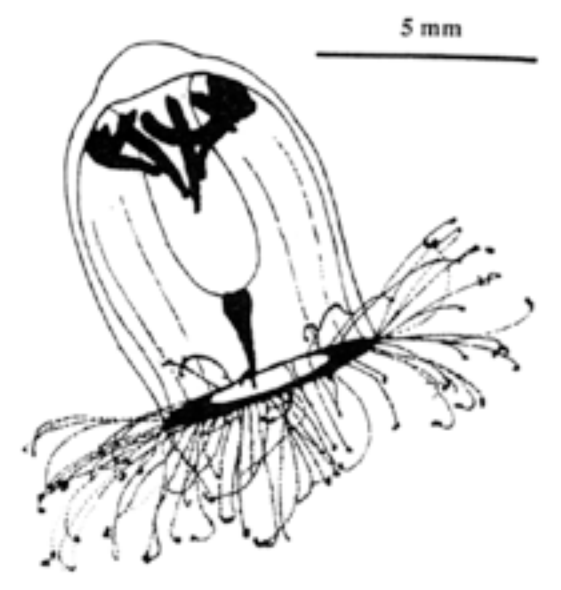


Raskoff/MPC

Aglantha swimming behaviour

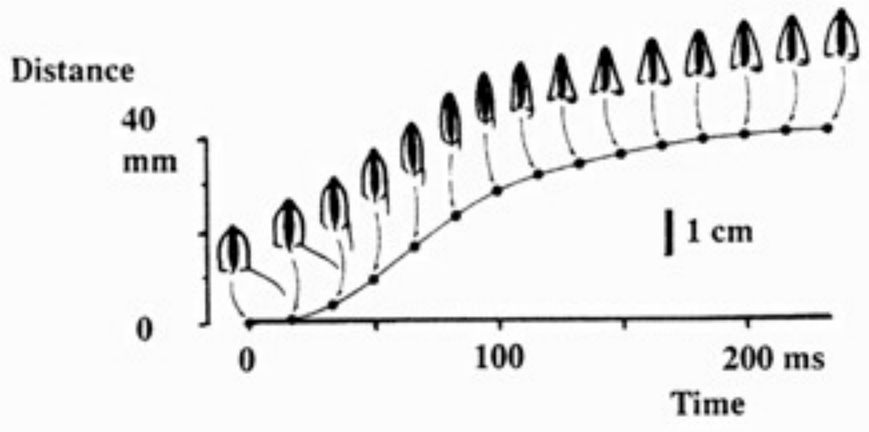


Slow Swimming (feeding)

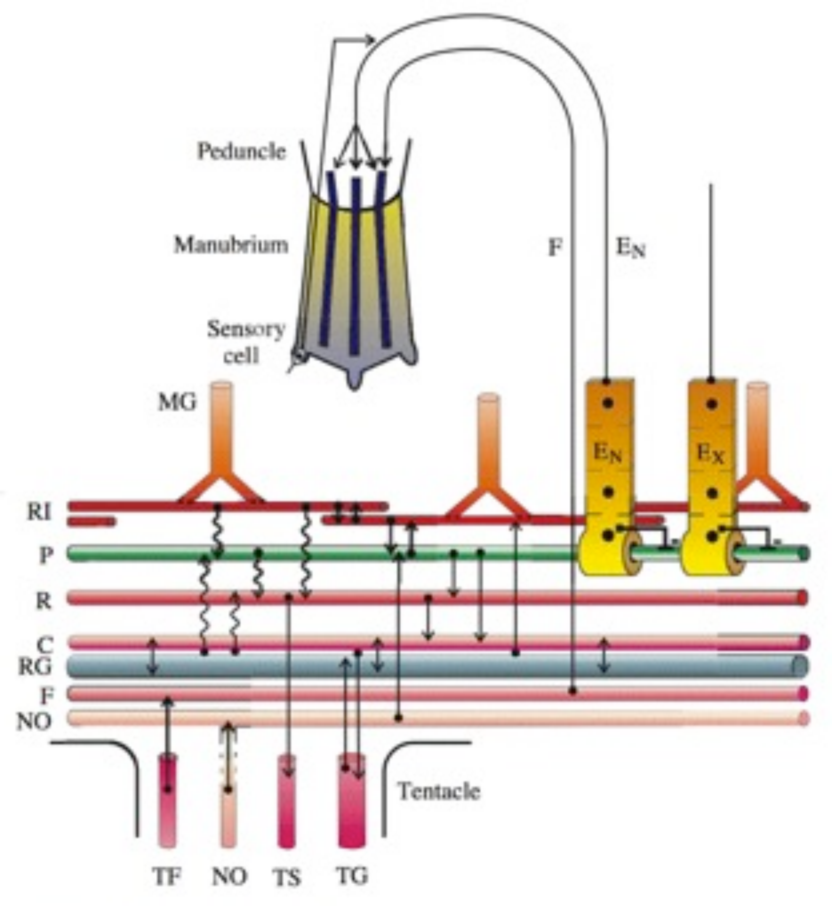


From Meech, 1995

Fast Escape



Aglantha Nervous System



Complex nervous system

12 distinct neuronal circuits

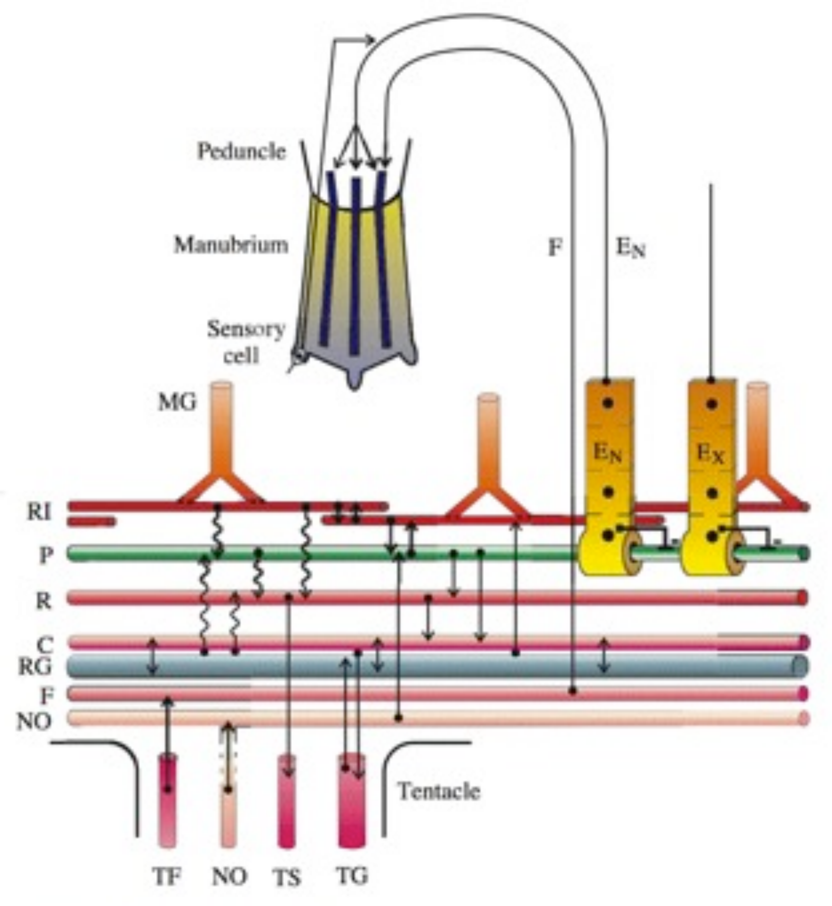
Two epithelial (cell-to-cell) systems

Most neural circuitry compressed into marginal nerve rings

"Slow swimming" (P + R) and "escape" (RG + TG) systems interact

(Mackie, 2004)

Aglantha Nervous System



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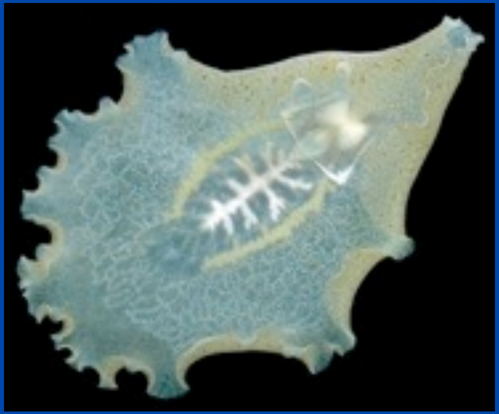
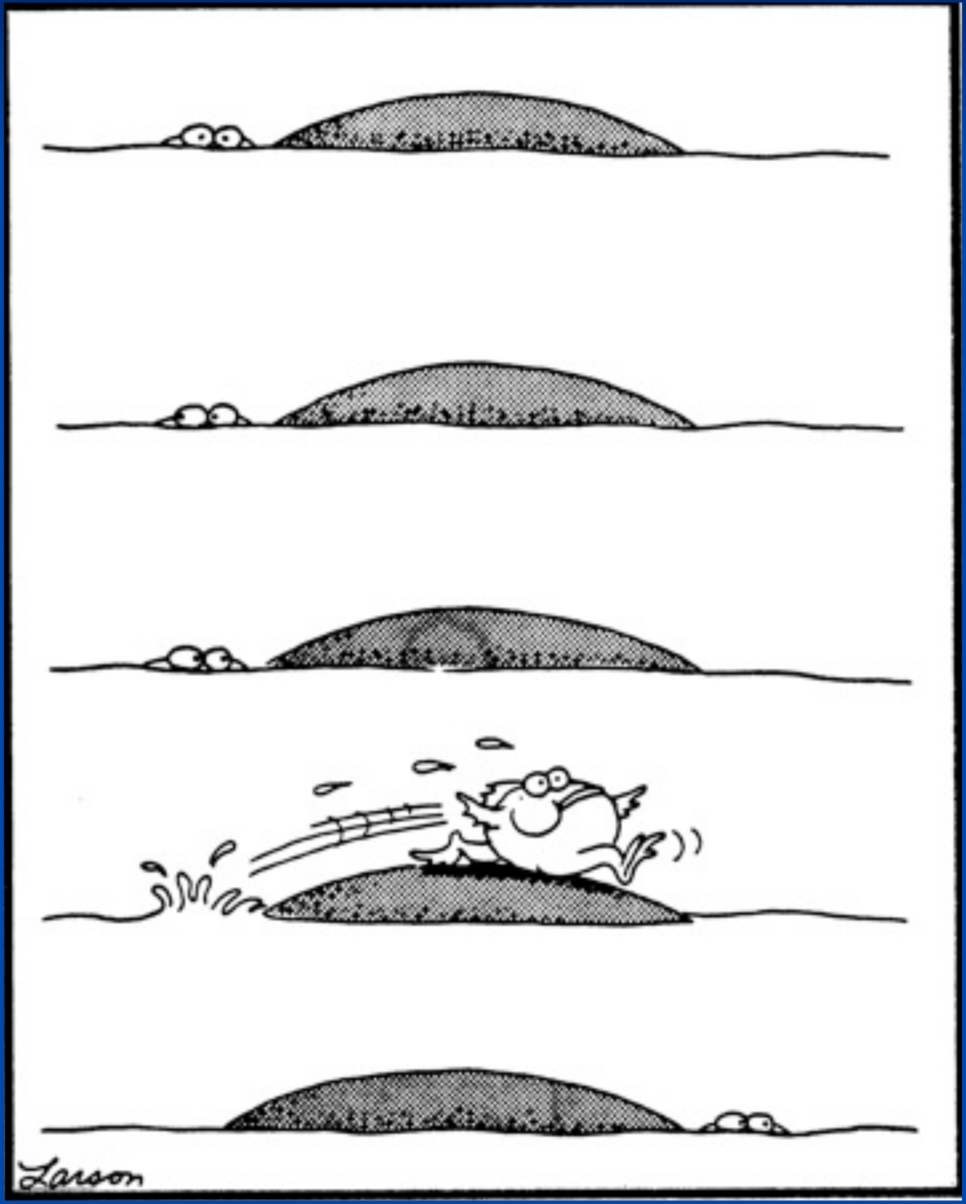
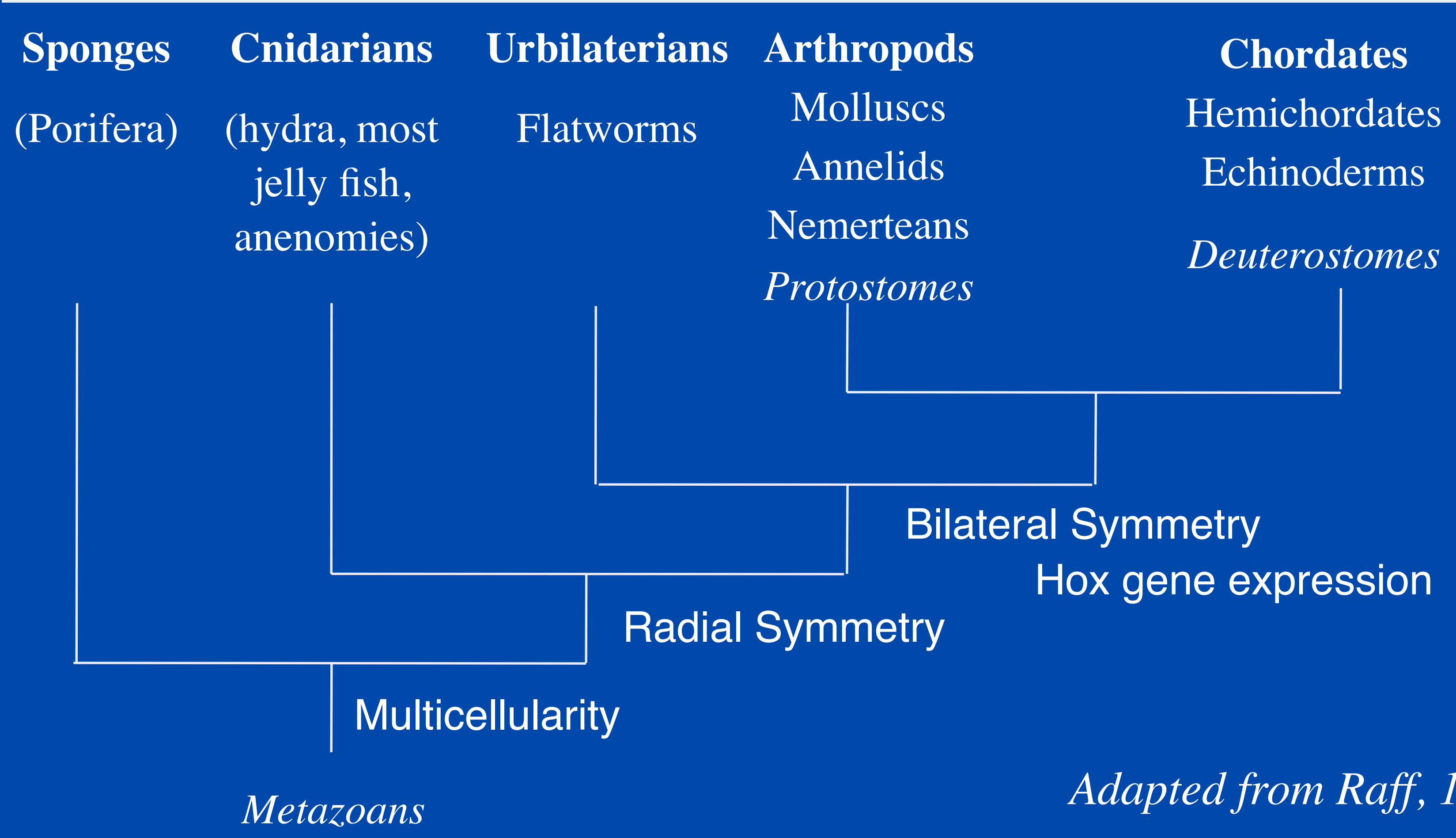
Great moments in evolution II

Flatworms





Brains and bilaterality



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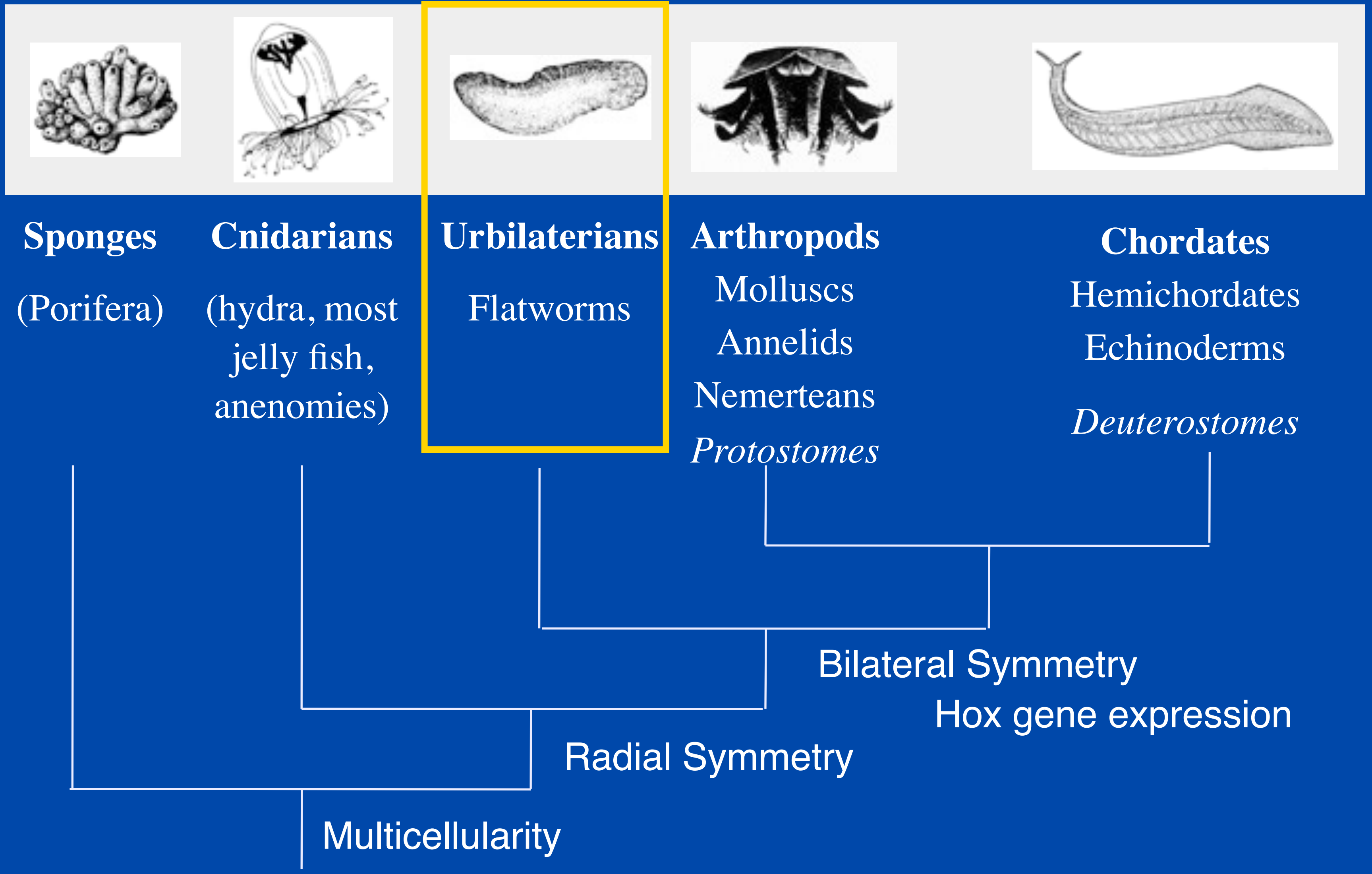

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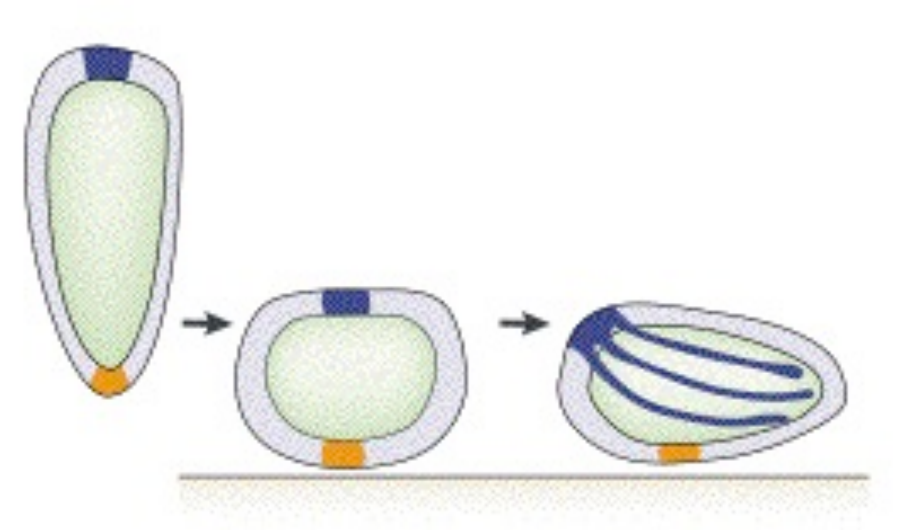
Urbilateria (c. 550mya)



Possible scenario for urbilaterian evolution from cnidarian larva (planula)

After Holland, 2003

Definitely:

anterior-posterior axis

two-ended gut

internal organs

simple nervous and sensory systems

Possibly:

internal body cavity (coelum)

simple tentacle-like appendages

Genetically:

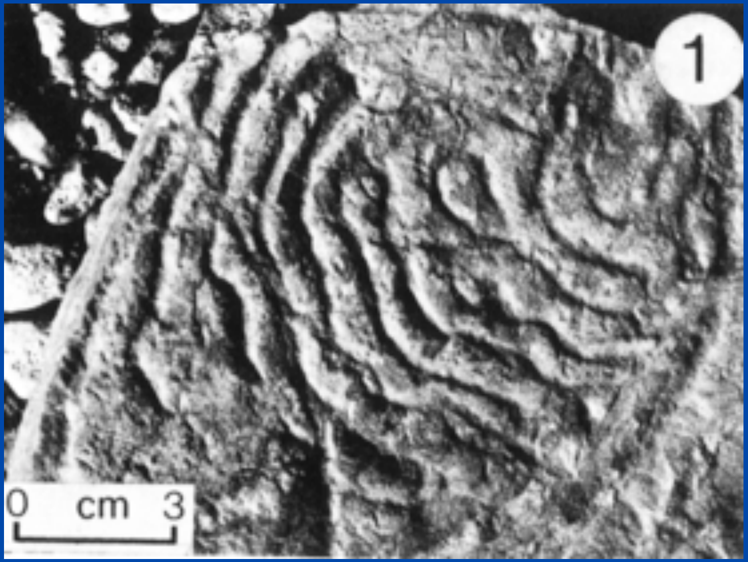
the “essential bilaterian toolbox” (e.g. Hox regulatory genes)

(Baguna et al., 2001; Erwin & Davidson, 2002; Knoll & Carroll, 1999)

Precambrian trace fossils

‘Scribbles’
(Seilacher, 67)

‘Tight’ meander
(Seilacher, 67)

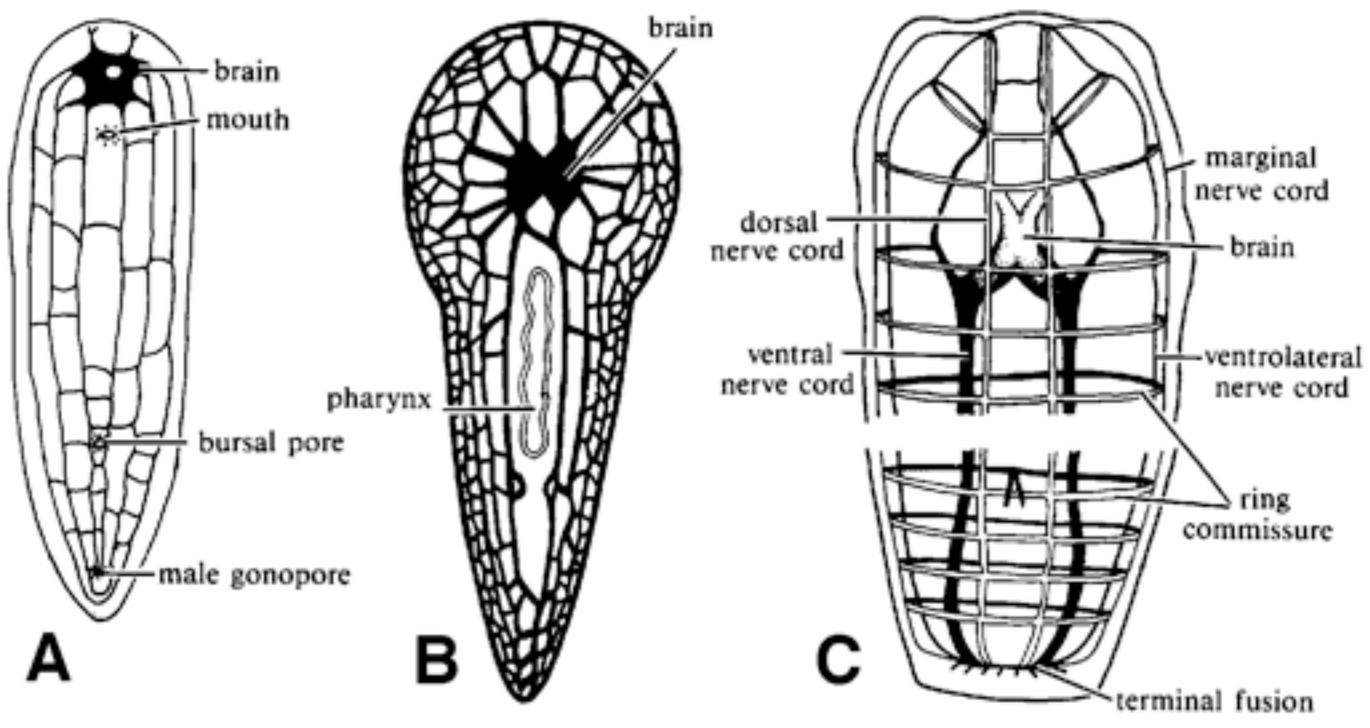


Precambrian meander
(Crimes and Anderson, 1985)

Free-living marine flatworms

Flatworm nervous systems

More primitive forms (A, B) show a more radial pattern, later forms (C) are more strongly bilateral

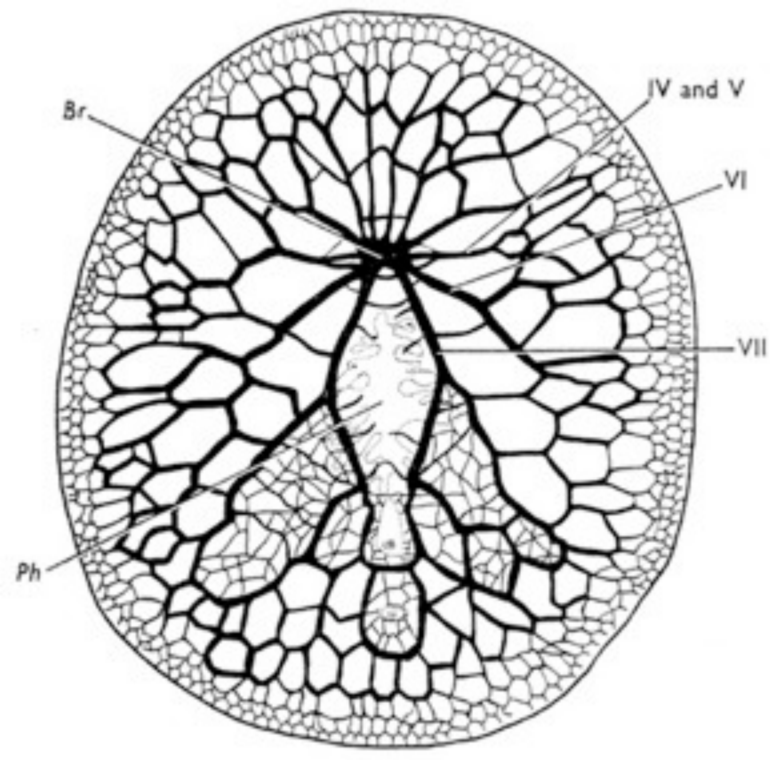


From Meglistch, 1991

The role of the flatworm brain in behaviour (1)

Following brain removal, components of both normal swimming and normal crawling are present but that these are never integrated into the normal sequences—the overall movement of the animal is irregular and uncoordinated.

Similarly, decerebrate animals lack a normal rapid righting response, although they can eventually right themselves by making writhing and twisting movements.

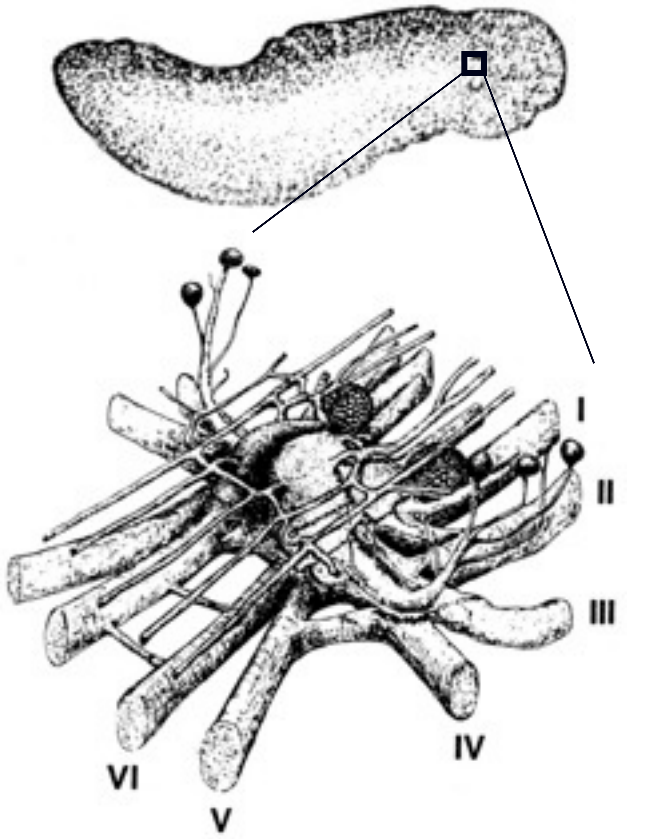


4cm

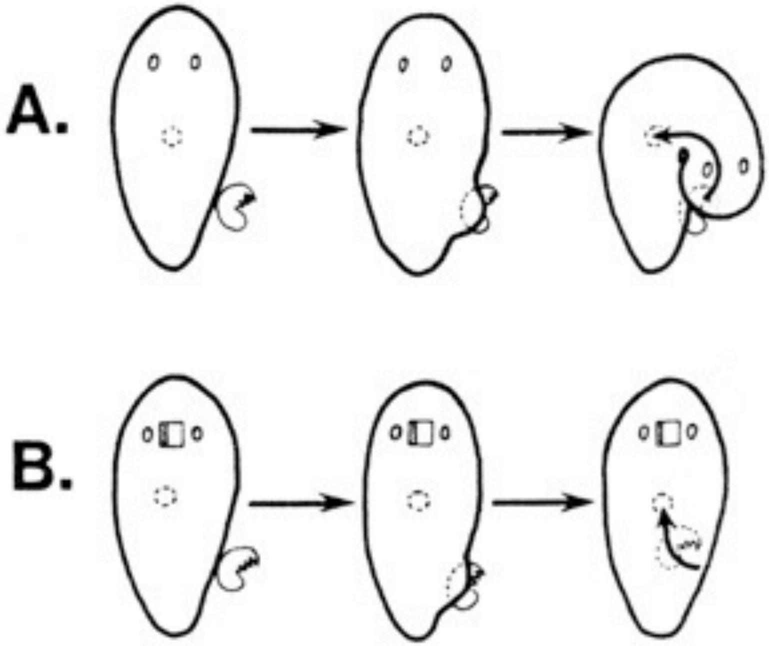
Planocera Gilchristi

From Gruber and Ewer, 1962

The role of the flatworm brain in behaviour (2)



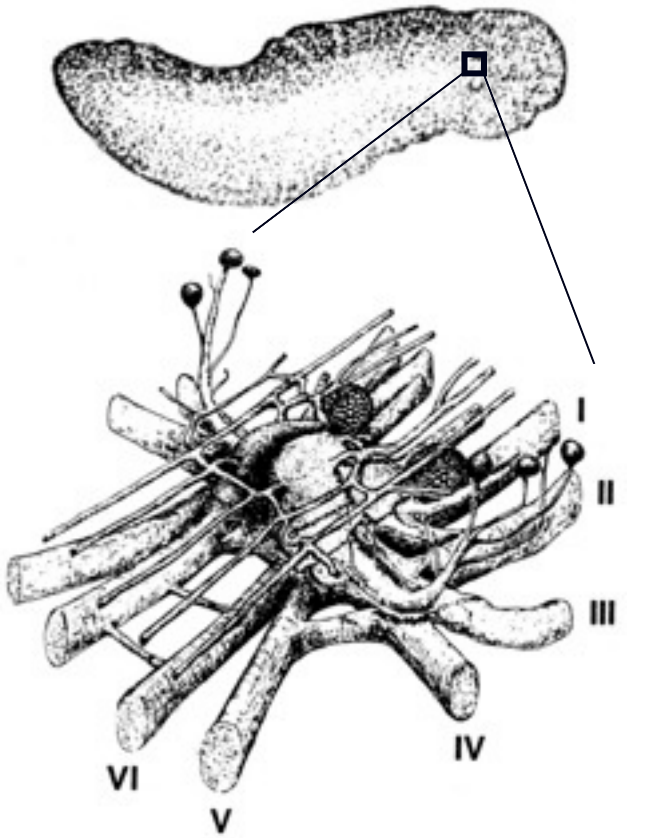
Notoplana Acticola



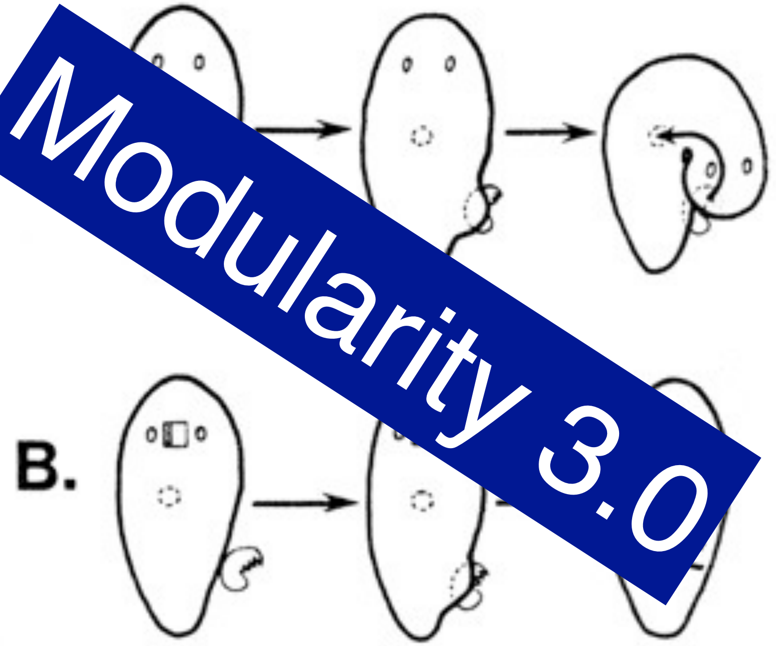
Typical feeding behaviour of normal and decerebrate worms

From Koopowitz and Keenan, 1982

The role of the flatworm brain in behaviour (2)



Notoplana Acticola

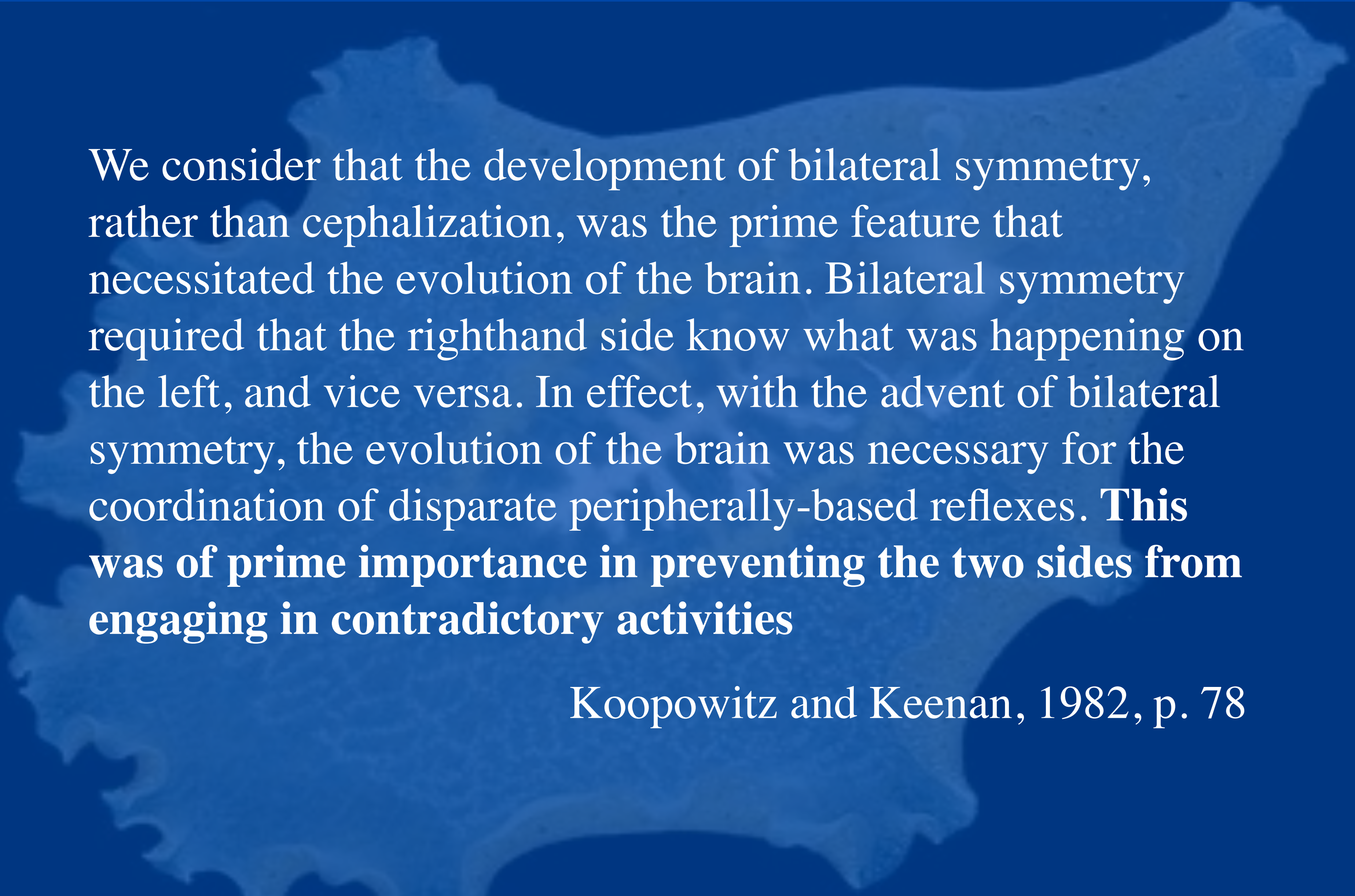


Modularity 3.0

Typical feeding behaviour of normal and decerebrate worms

From Koopowitz and Keenan, 1982

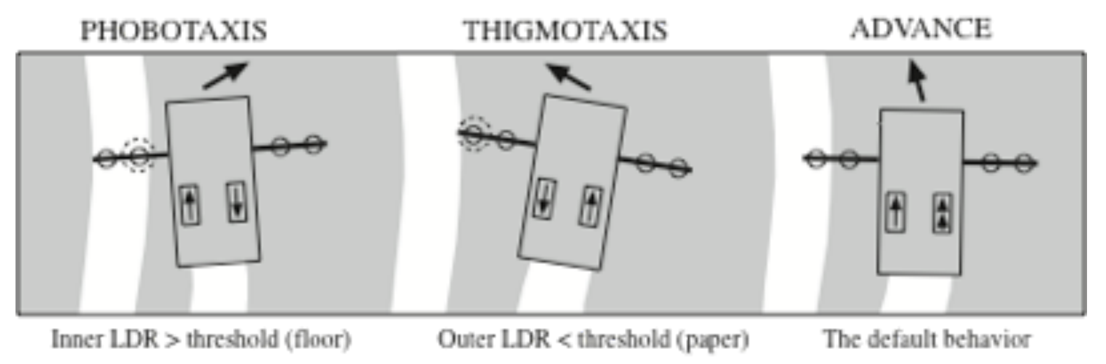
The early brain as an action selector

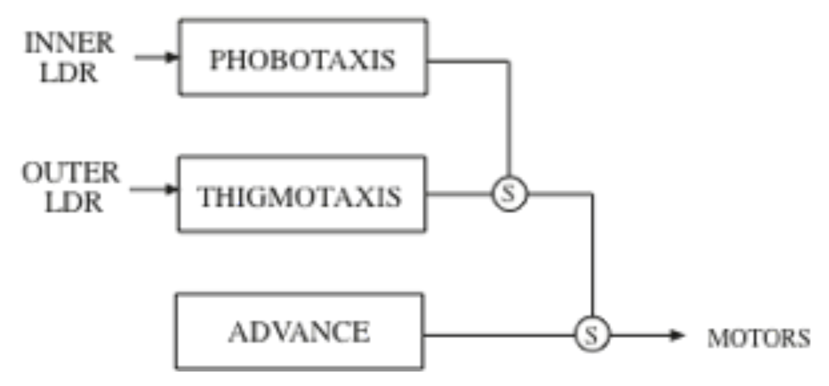


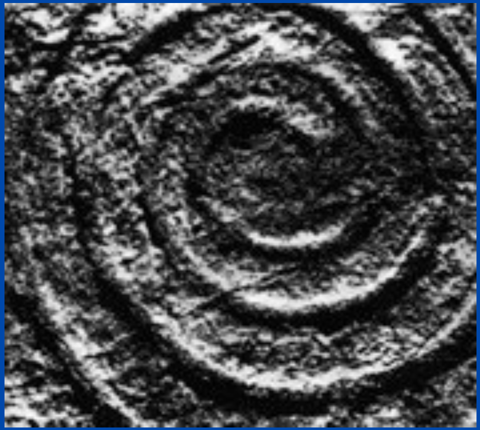
We consider that the development of bilateral symmetry, rather than cephalization, was the prime feature that necessitated the evolution of the brain. Bilateral symmetry required that the righthand side know what was happening on the left, and vice versa. In effect, with the advent of bilateral symmetry, the evolution of the brain was necessary for the coordination of disparate peripherally-based reflexes. **This was of prime importance in preventing the two sides from engaging in contradictory activities**

Koopowitz and Keenan, 1982, p. 78

Modelling a spiral trace-maker



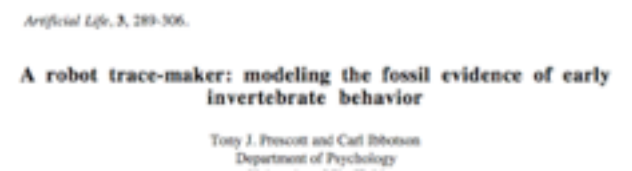




Spirodesmos (Huckriede, 1952)

Thigmotaxis—stay close to tracks

Phobotaxis—avoid recrossing tracks



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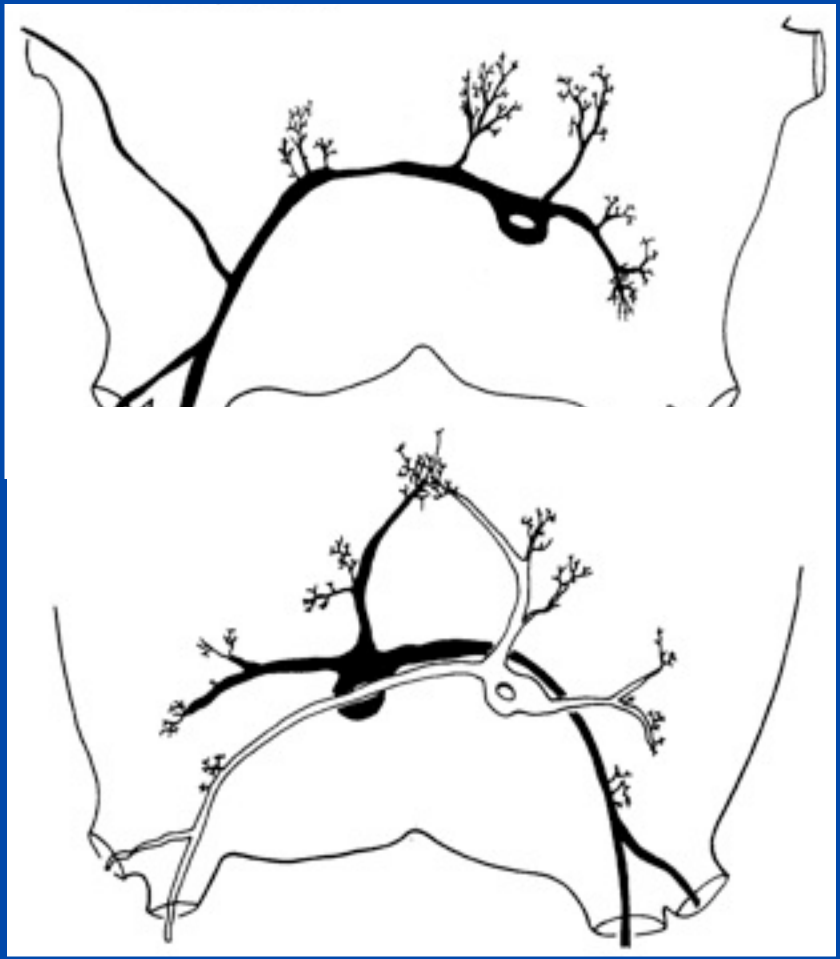
Decussating neurons in flatworm brains



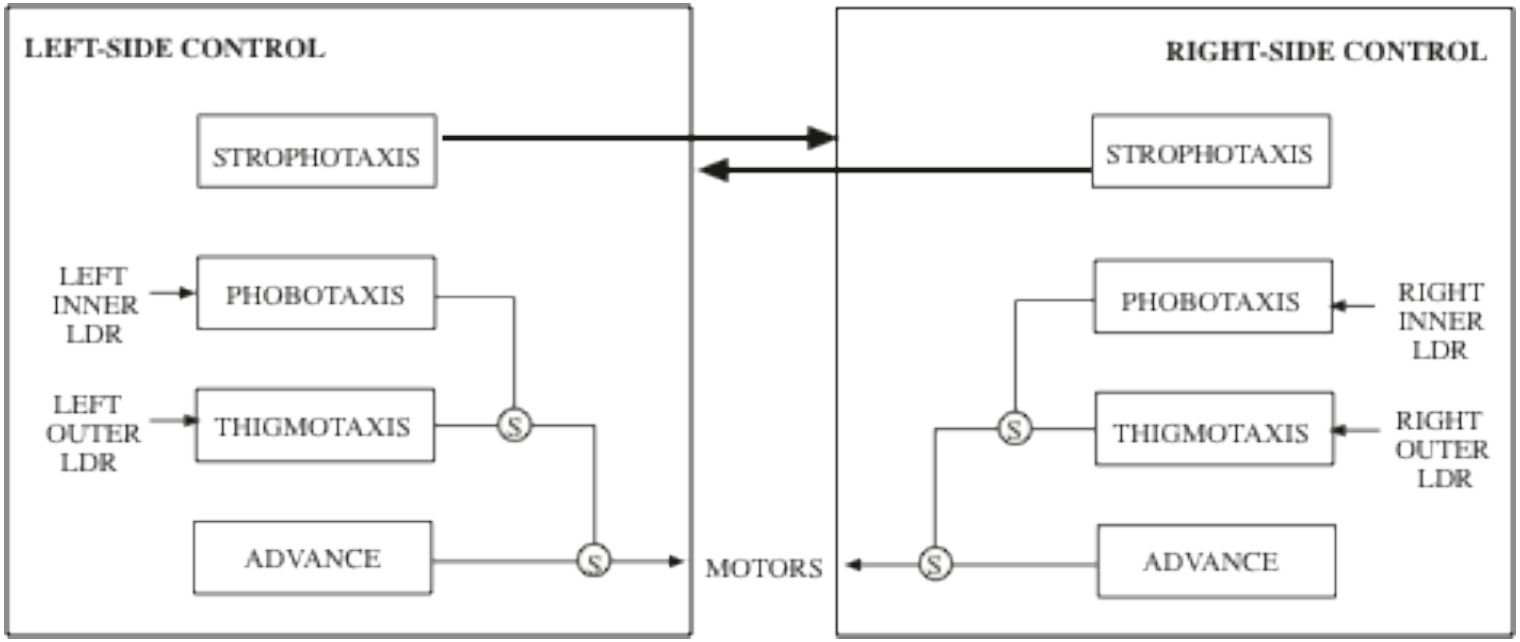
Dye-stained neurons in Notoplana acticola, from Koopowitz, 1986

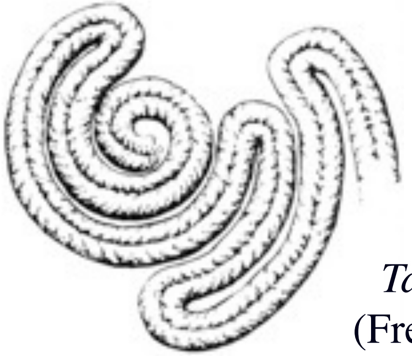
Top: **decussating** neurons—cells whose soma and dendrites are found in one half of the brain while their axons project across the midline to peripheral targets on the other side

Bottom: **Dye-coupled** neurons. Some decussating neurons are electrotonically coupled with symmetrical cells on the opposite side of the midline (so they work in unison)

Could provide a key element of the substrate for maintaining behavioral coherence between the two halves of the body: non-coupled neurons suppress or facilitate responses in the opposite body-half; coupled neurons ensure synchrony between the two sides

Modelling a meandering trace-maker

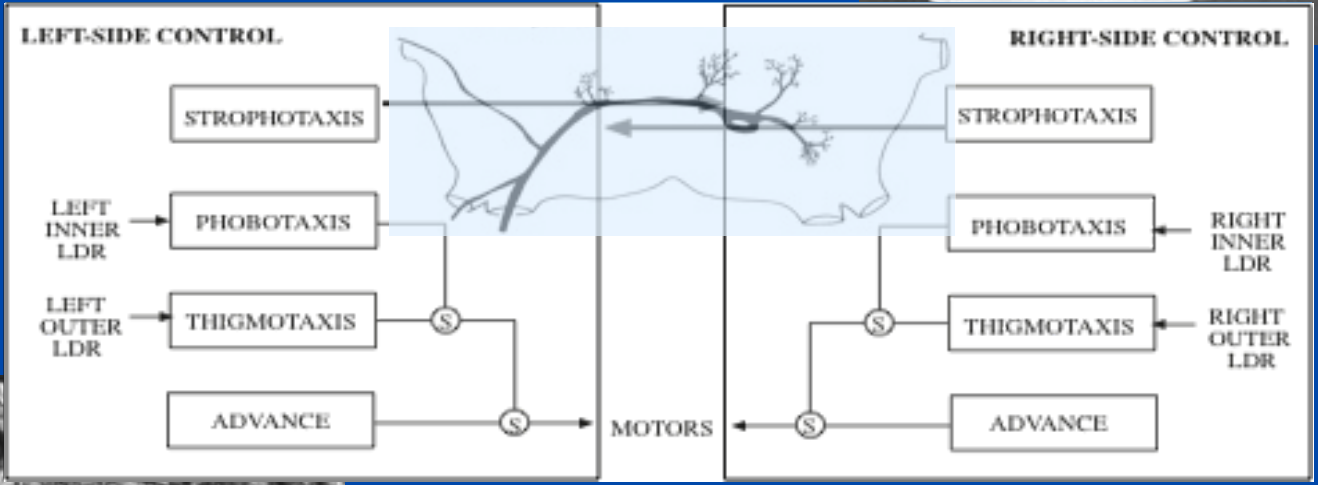




Taphrelminthopsis
(Frey & Seilacher,80)

Precambrian trace-makers reconsidered

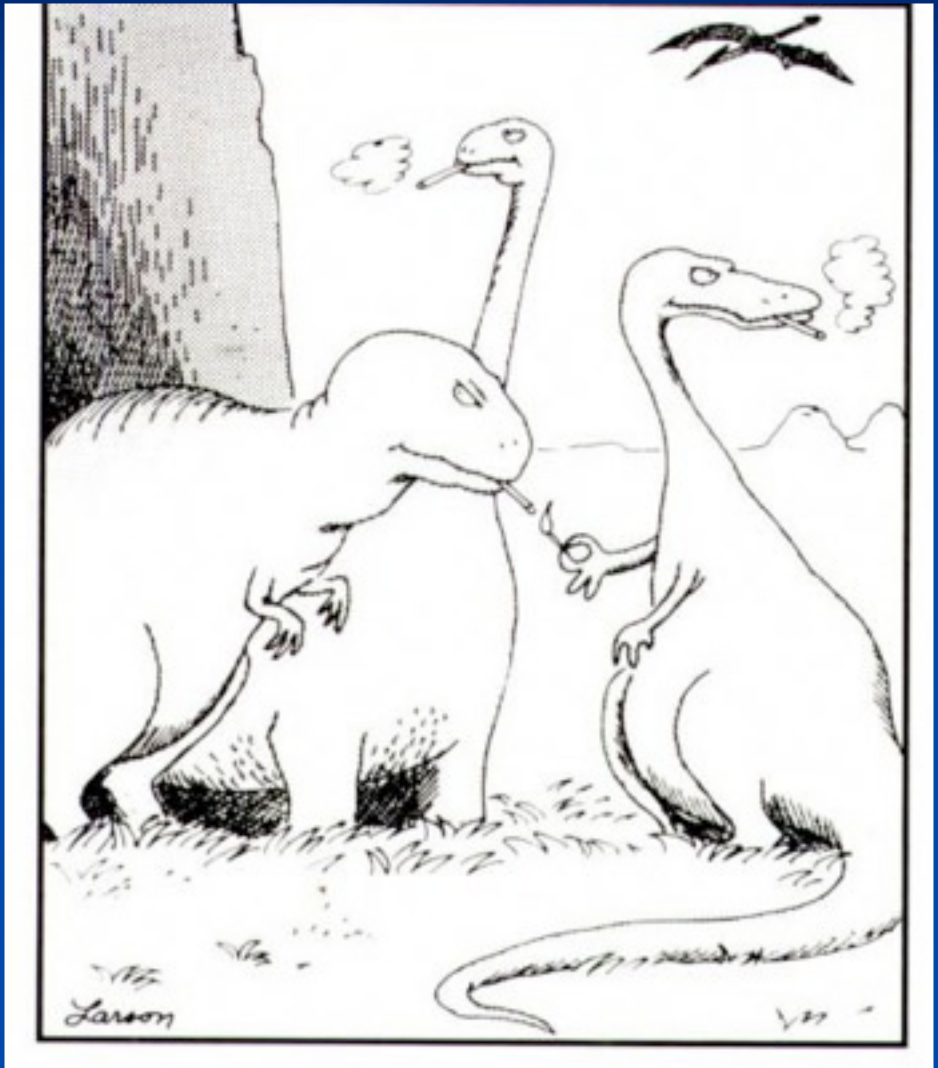
Thigmotaxis and phobotaxis are reflexive mechanisms associated with peripheral sensors. Strophotaxis determines which side of the body is actively controlling the motor system…



Does the appearance of efficient foraging trails in the fossil records of the late precambrian mark the point where centralized action selection mechanisms evolved to take control over peripheral reflexive systems?

Great moments in nervous system evolution III

Vertebrates



The real reason dinosaurs became extinct

Vertebrate nervous systems

Sponges

(Porifera)

Cnidarians

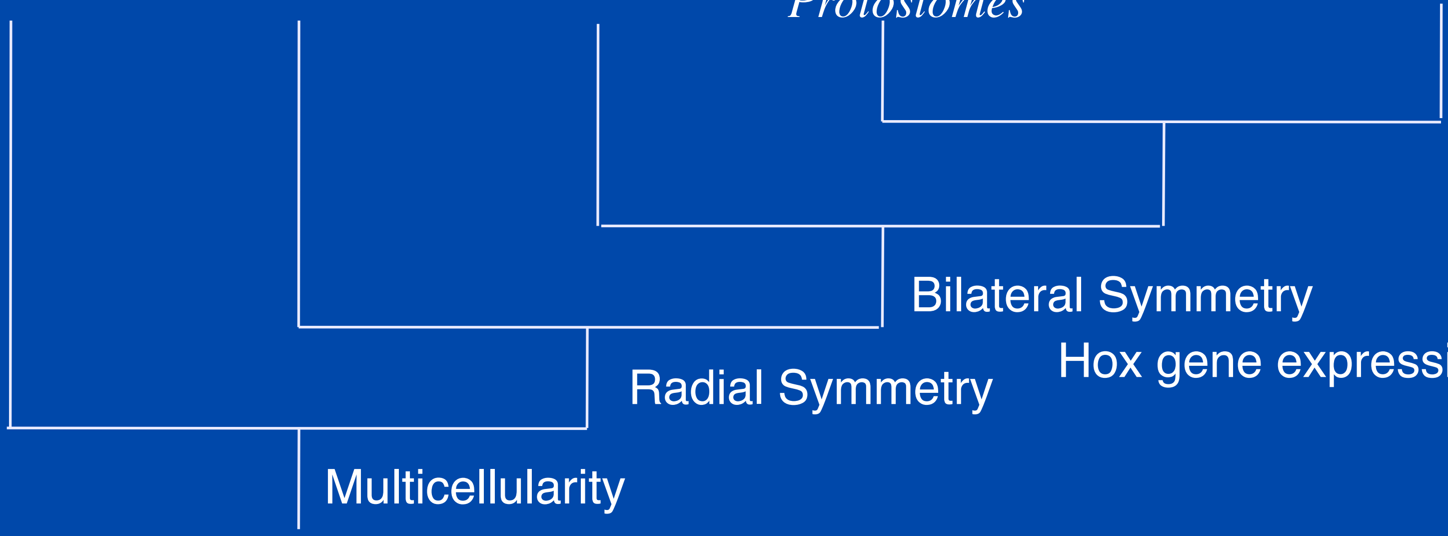
(hydra, most jelly fish, anenomies)

Flatworms

(Platy-helminthes)

Arthropods
Molluscs
Annelids
Nemerteans
Protostomes

Chordates
Inc. Vertebrates
Echinoderms
Deuterostomes



Bilateral Symmetry

Hox gene expression

Radial Symmetry

Multicellularity

Metazoans

Adapted from Raff, 1996

Vertebrate nervous systems

Sponges

(Porifera)

Cnidarians

(hydra, most jelly fish, anenomies)

Flatworms

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Molluscs

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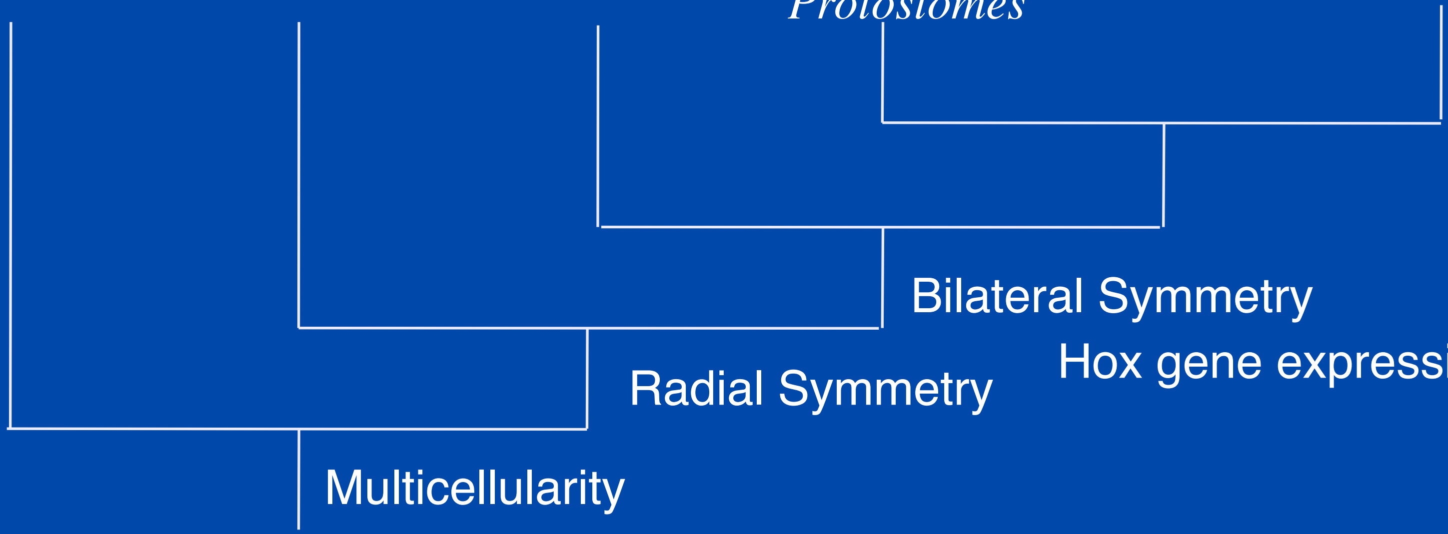
Inc. Vertebrates

Echinoderms

Deuterostomes



Bilateral Symmetry

Hox gene expression

Radial Symmetry

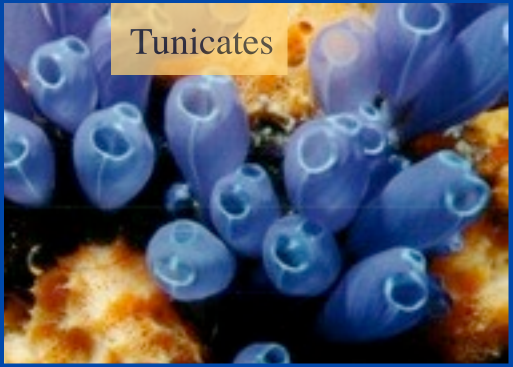
Multicellularity

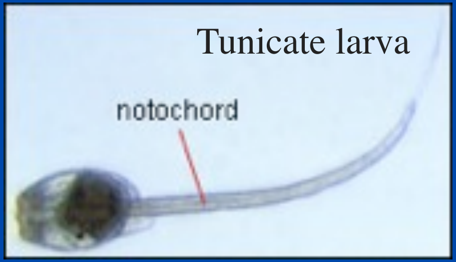
Metazoans

Adapted from Raff, 1996

Deuterostomes (non vertebrate)

Echinoderms -
Pentameral Symmetry

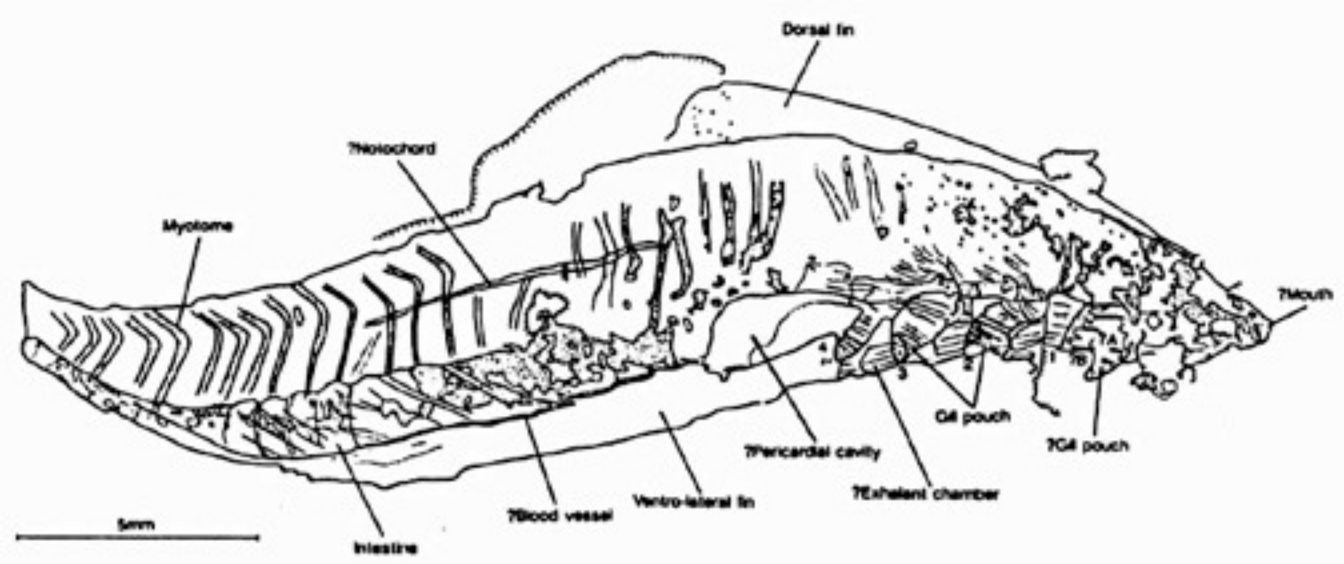




Chordates

First Vertebrates

Left: Fossil of an early vertebrate *Haikouichthys*. Right: Lamphrey in various stages of decay



From Shu et al., 1999

Sansom et al. 2010

First Vertebrates

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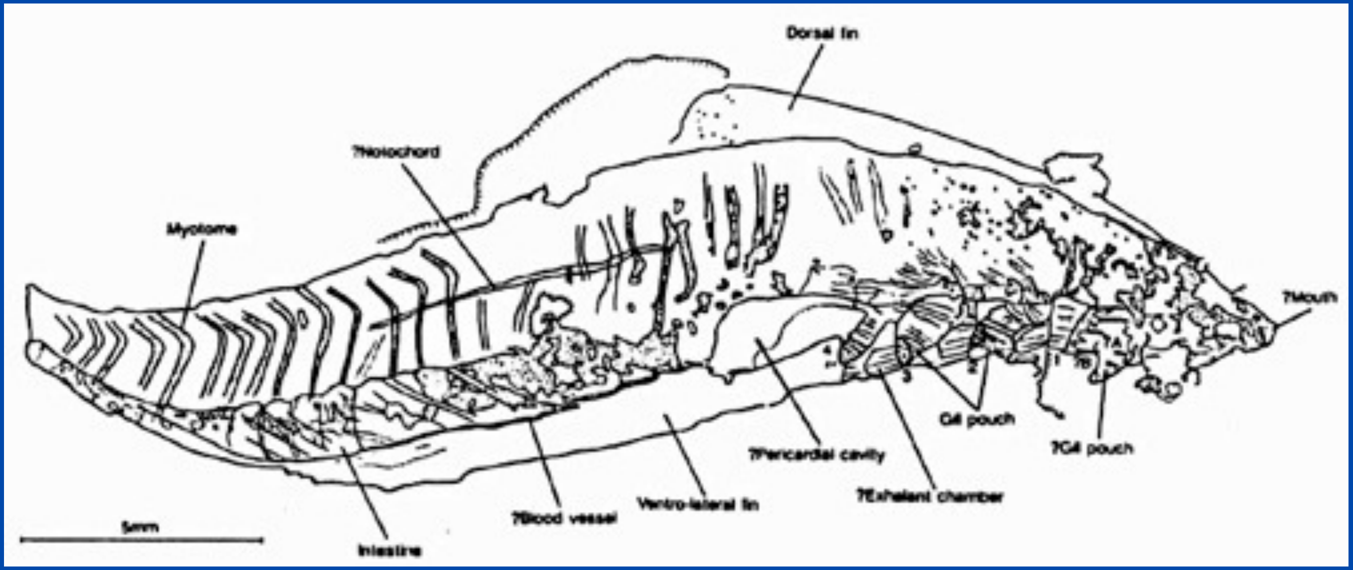
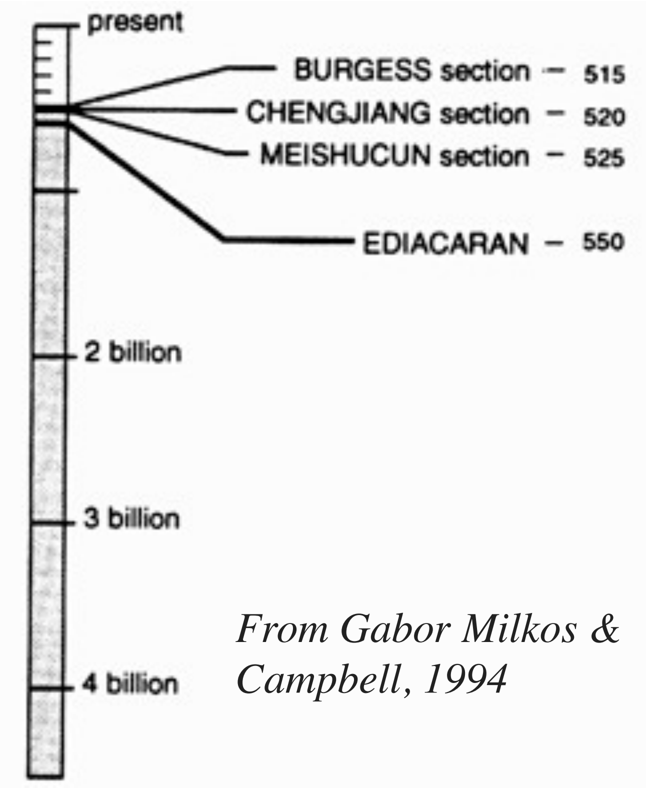


From Shu et al., 1999

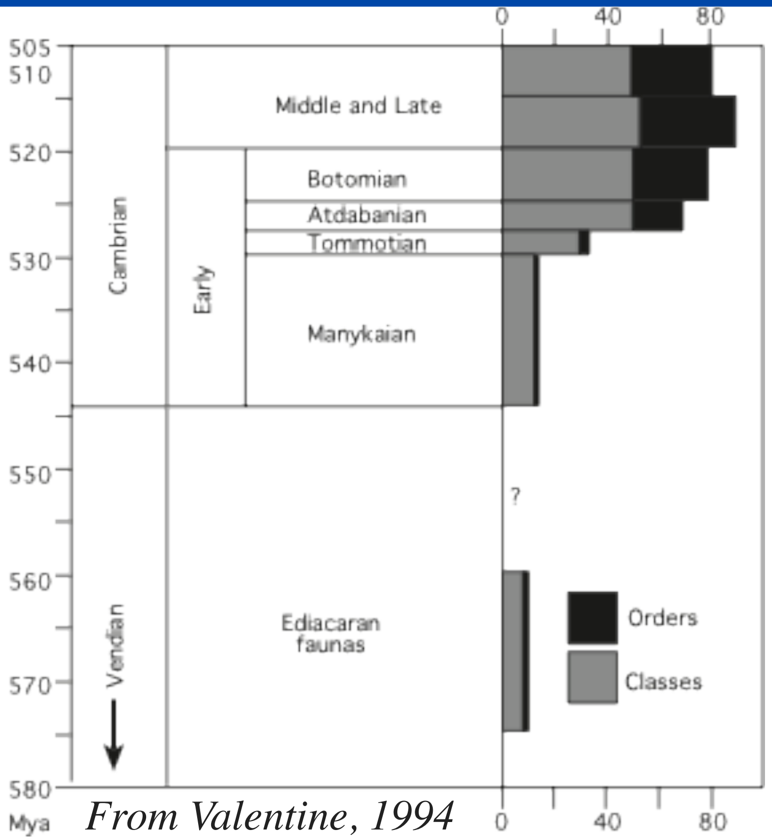
Sansom et al. 2010

520 million years old
(from the Lower Cambrian Chengjiang fauna)

Evolutionary time



From Gabor Milkos & Campbell, 1994

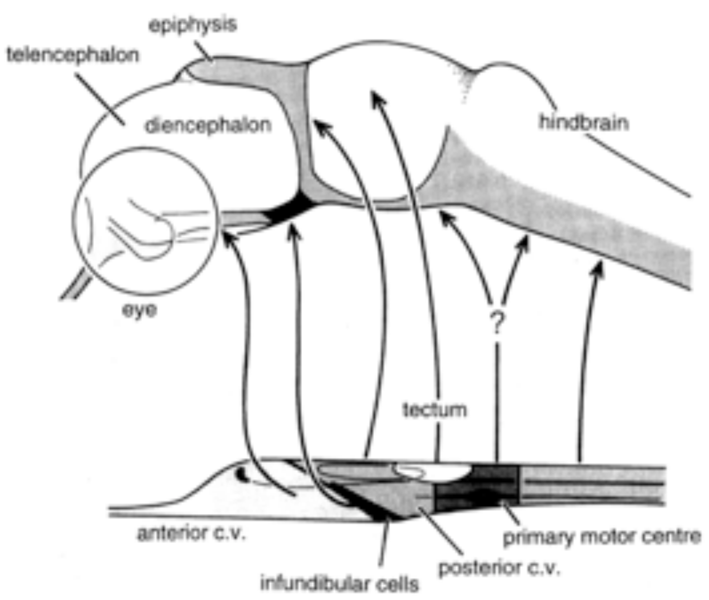


From Valentine, 1994

Complex brains were unlikely to have been painstakingly "wired-up" synapse by synapse over hundreds of millions of years. We are faced with the exciting prospect that nervous systems can be constructed rapidly

George Gabor Miklos, 1993

Early vertebrate brains

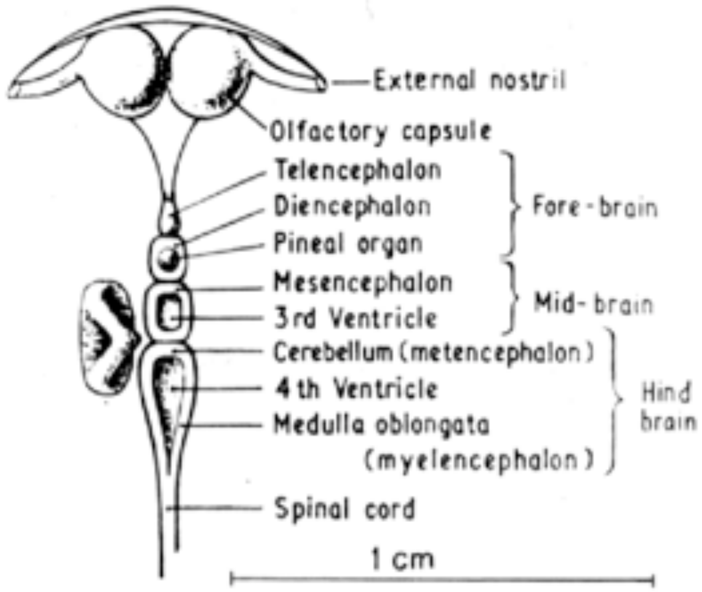


Above: The brain of Amphioxus (*Branchiostoma*)— said to resemble a transitional stage between ancestral chordate and vertebrate.

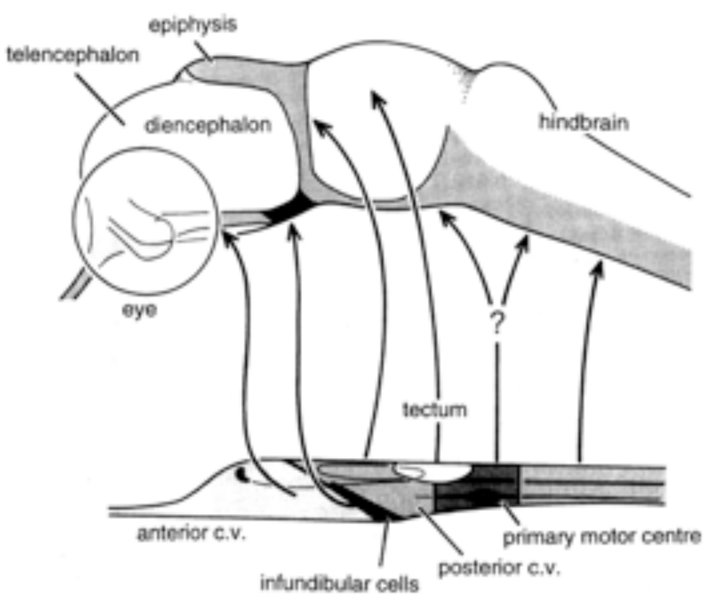
From Lacalli, 1996

Below: Reconstruction of the CNS of an early jawless fish from a fossilized endocast about 400 million years old.

From Halstead Tarlo (1965)



Early vertebrate brains



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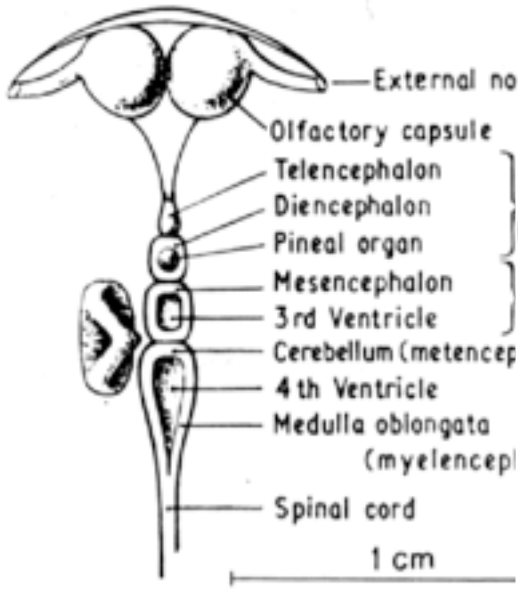
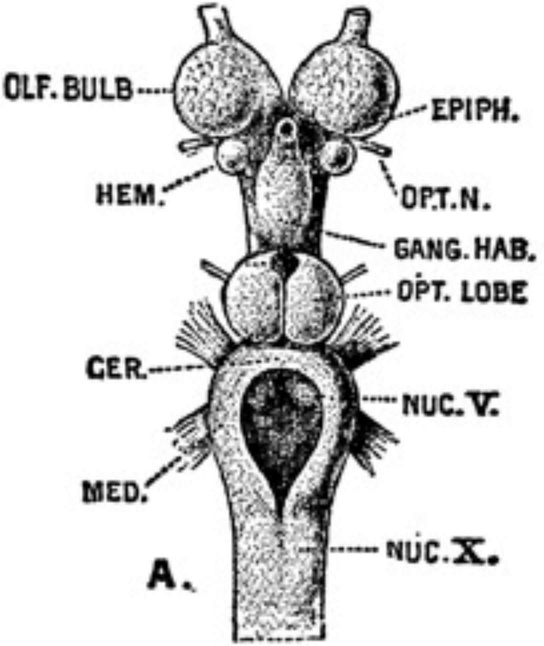
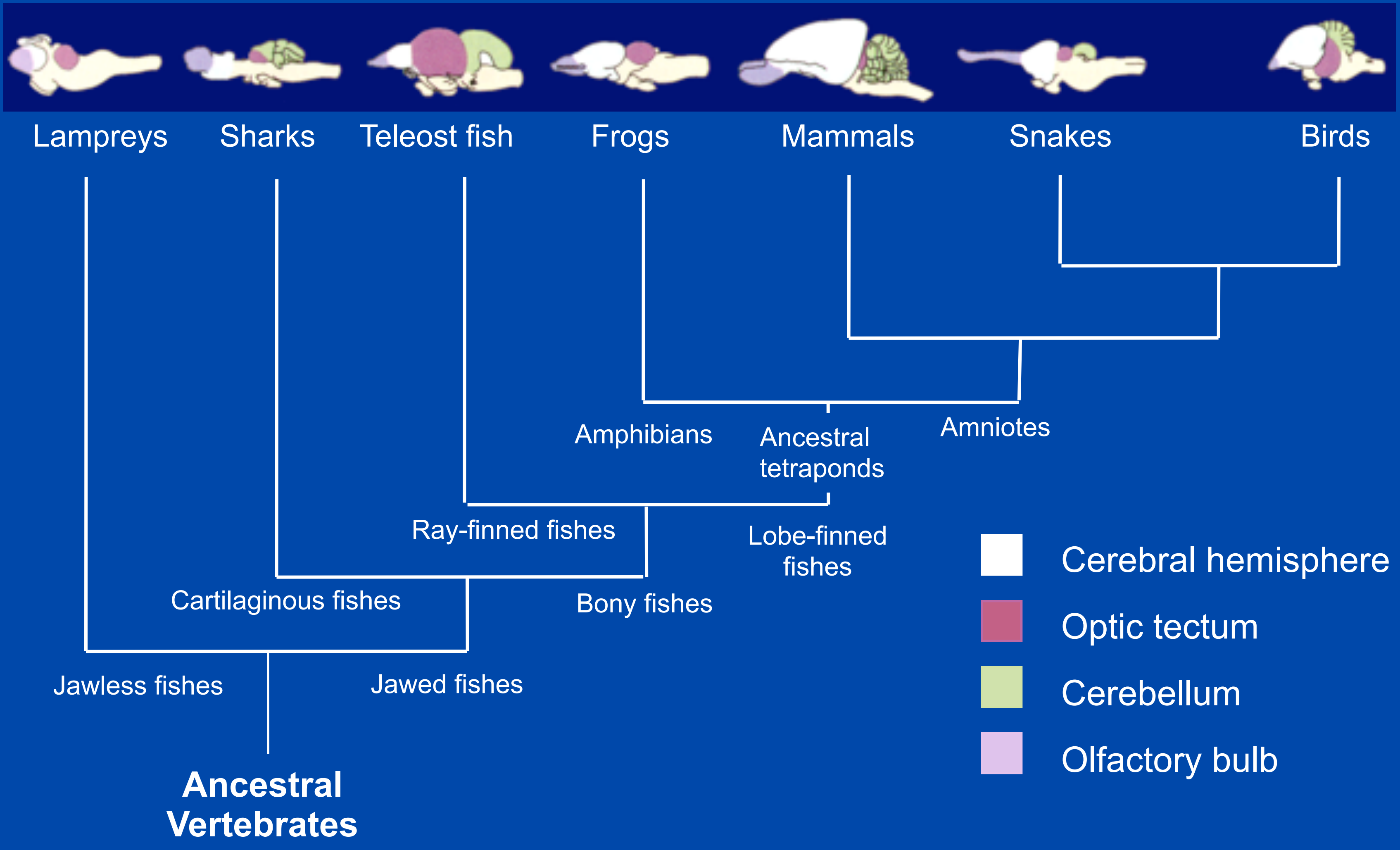




Brain of a lamphrey

Modern vertebrate brains: diverse shapes and sizes, common structures



Lampreys

Sharks

Teleost fish

Frogs

Mammals

Snakes

Birds

Amphibians

Ancestral tetraponds

Amniotes

Ray-finned fishes

Lobe-finned fishes

Cartilaginous fishes

Bony fishes

Jawless fishes

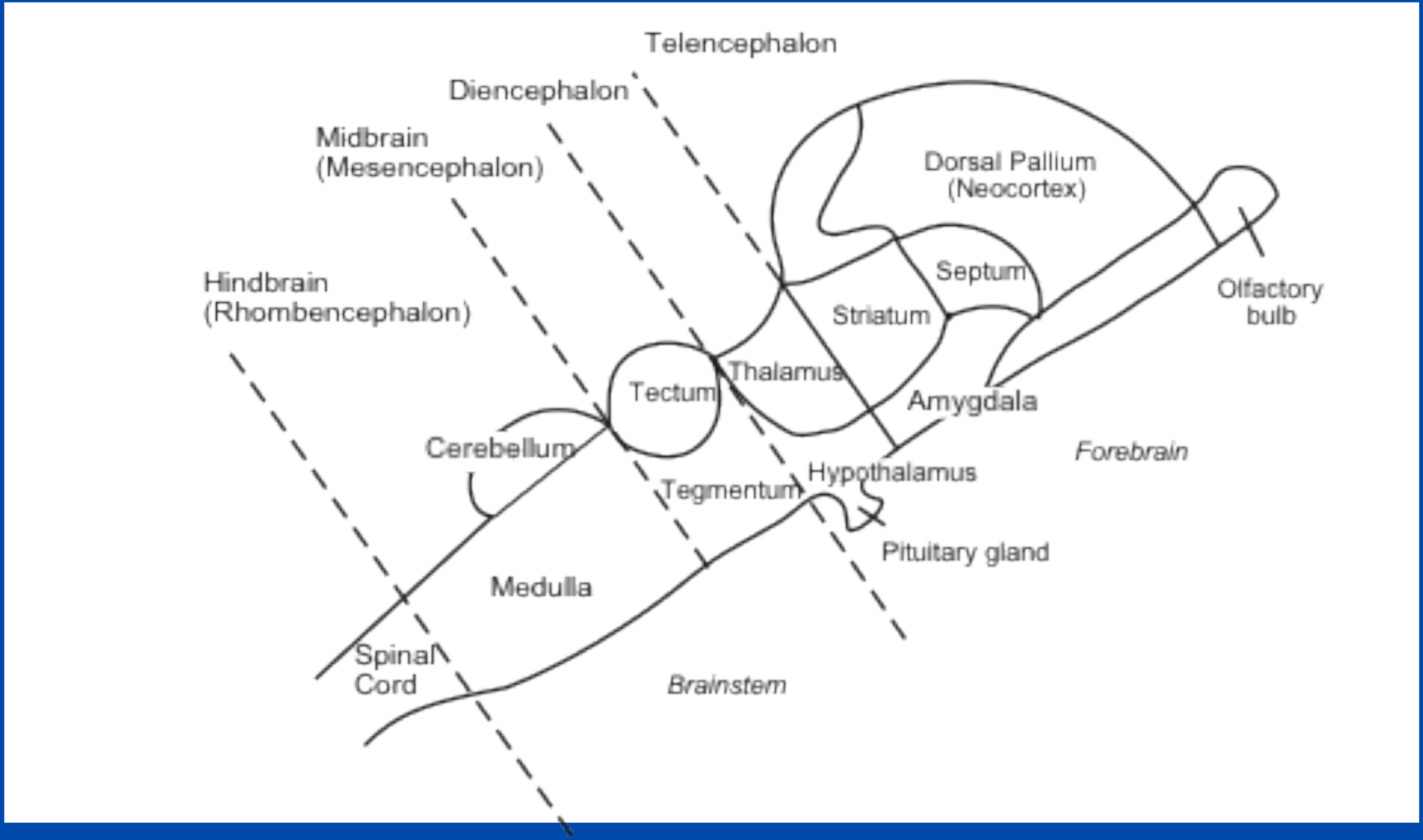
Jawed fishes

Ancestral Vertebrates

- ⬜ Cerebral hemisphere
- 🟥 Optic tectum
- 🟩 Cerebellum
- 🟪 Olfactory bulb

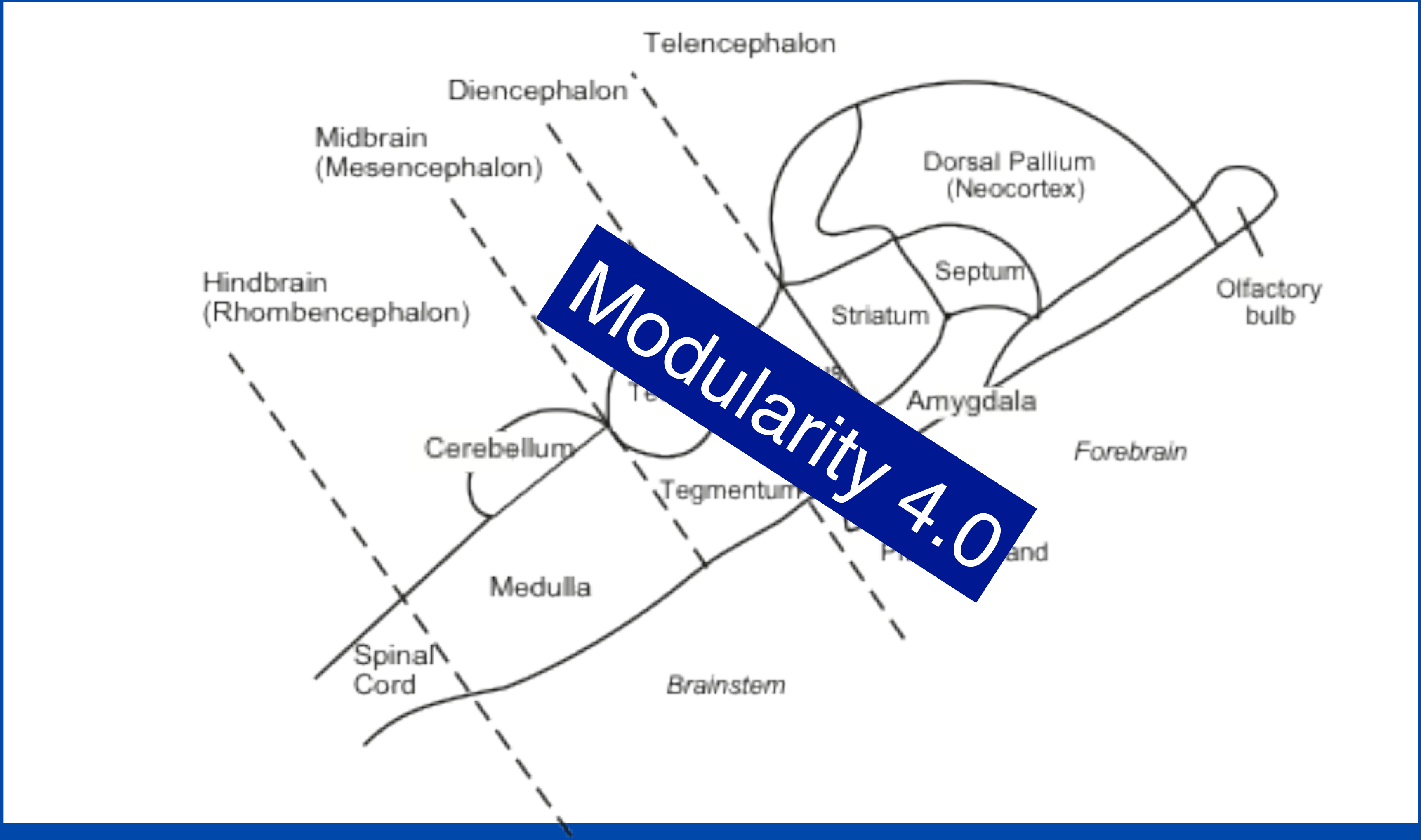
Adapted from Rosenzweig et al. 1999

Generic plan of the vertebrate brain



Based on Butler and Hodos, 1996

Generic plan of the vertebrate brain



Modularity 4.0

Based on Butler and Hodos, 1996

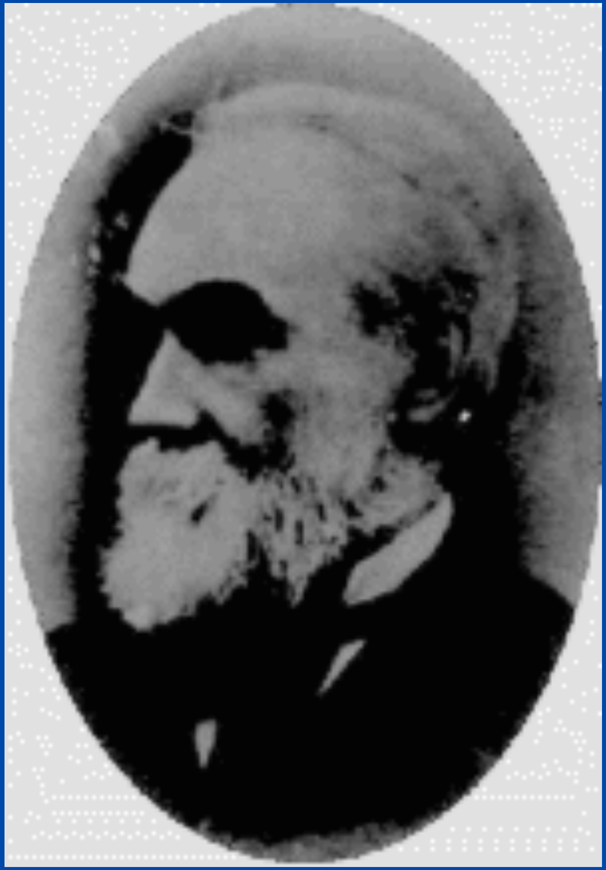
What changed with evolution?

- Size of specific brain structures
  - E.g. hippocampus in food-storing animals and birds
  - Cerebellum in electric fish
  - Cortex in mammals and primates
- Some new pathways added
  - E.g. cortico-spinal tract in mammals for fine-grained control of movement
- Areas became more or less differentiated
  - E.g. increase in number of cortical areas in primates
- Microstructural organisation
  - Migration of cell groups, addition of cell types, selective connection loss, axonal invasion of new areas

Organising principles I.
The brain as a layered architecture

"That the middle motor centers represent over again what all the lowest motor centers have represented, will be disputed by few. I go further, and say that the highest motor centers (frontal lobes) represent over again, in more complex combinations, what the middle motor centers represent."

From "The evolution and dissolution of the nervous system" (1884)



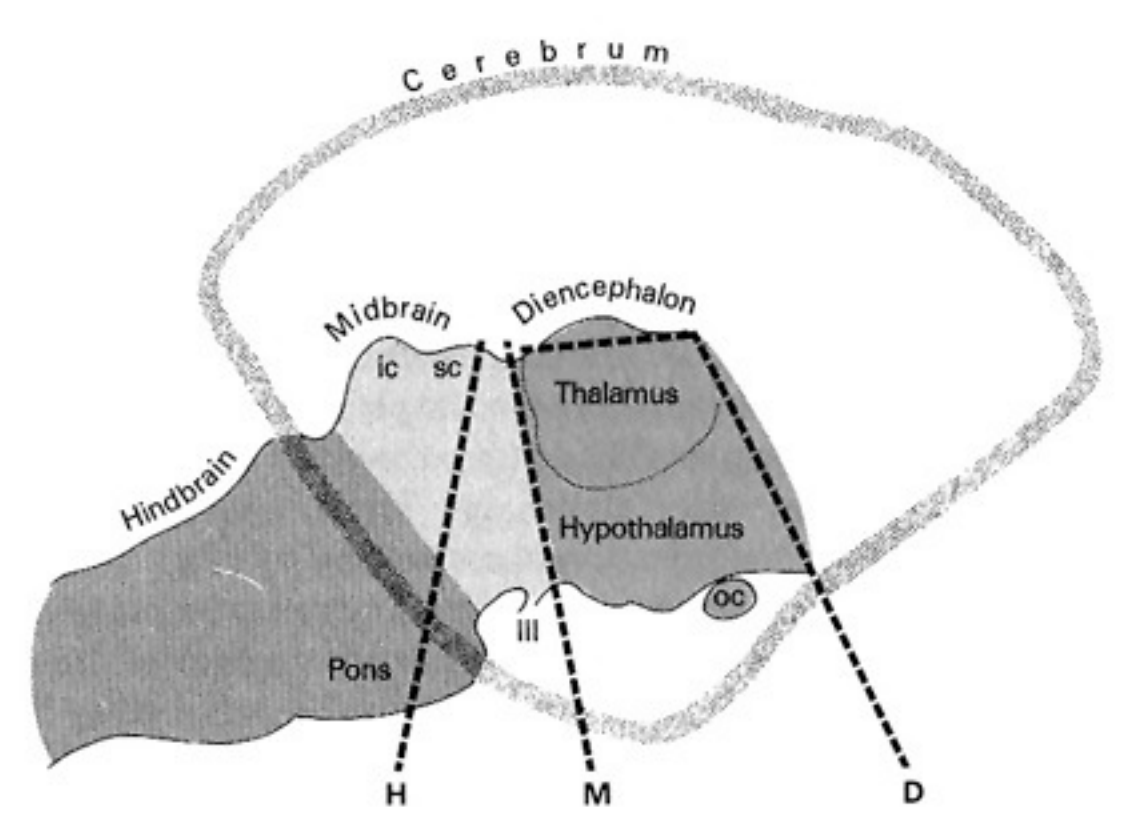
**John Hughlings Jackson
1835-1911**

Adaptive Behavior 1999, 7(1), 99-127

Layered Control Architectures in Robots and Vertebrates

TONY J. PRESCOTT, PETER REDGRAVE, AND KEVIN GURNEY
University of Sheffield, UK

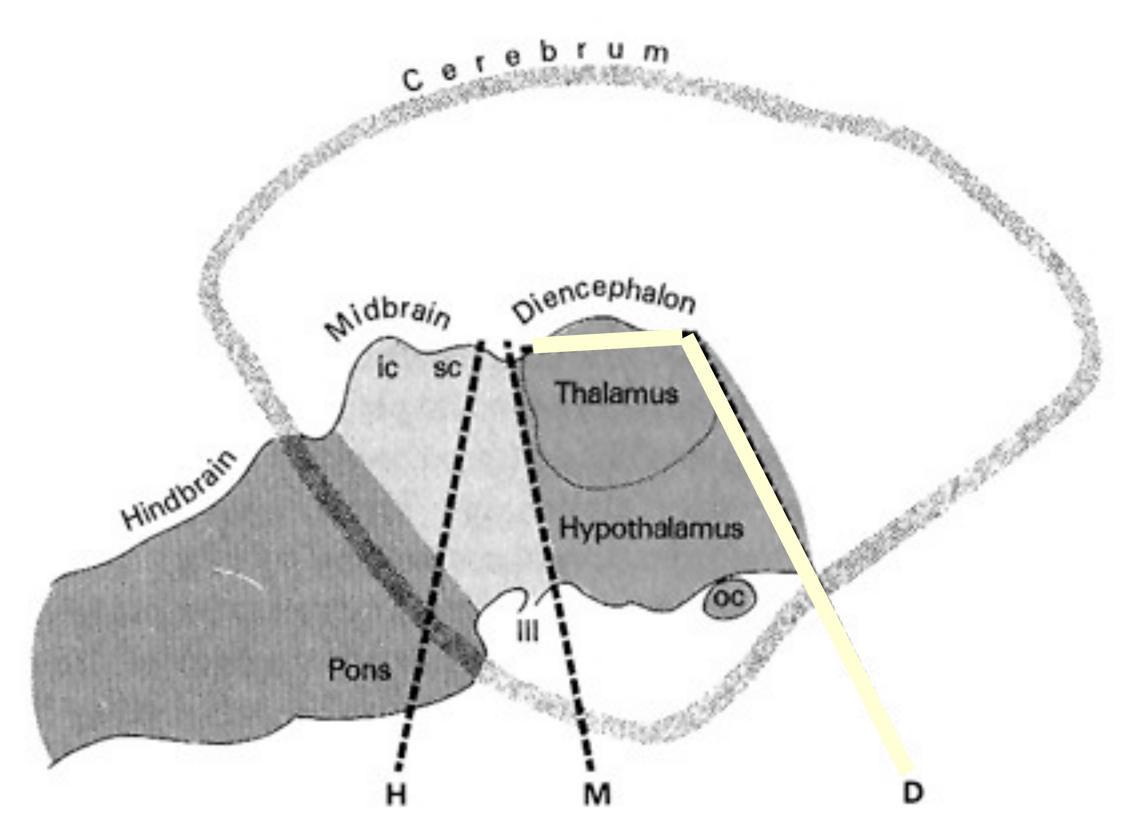
Transection studies



Transection studies

Diencephalic rat

generates motivated sequences



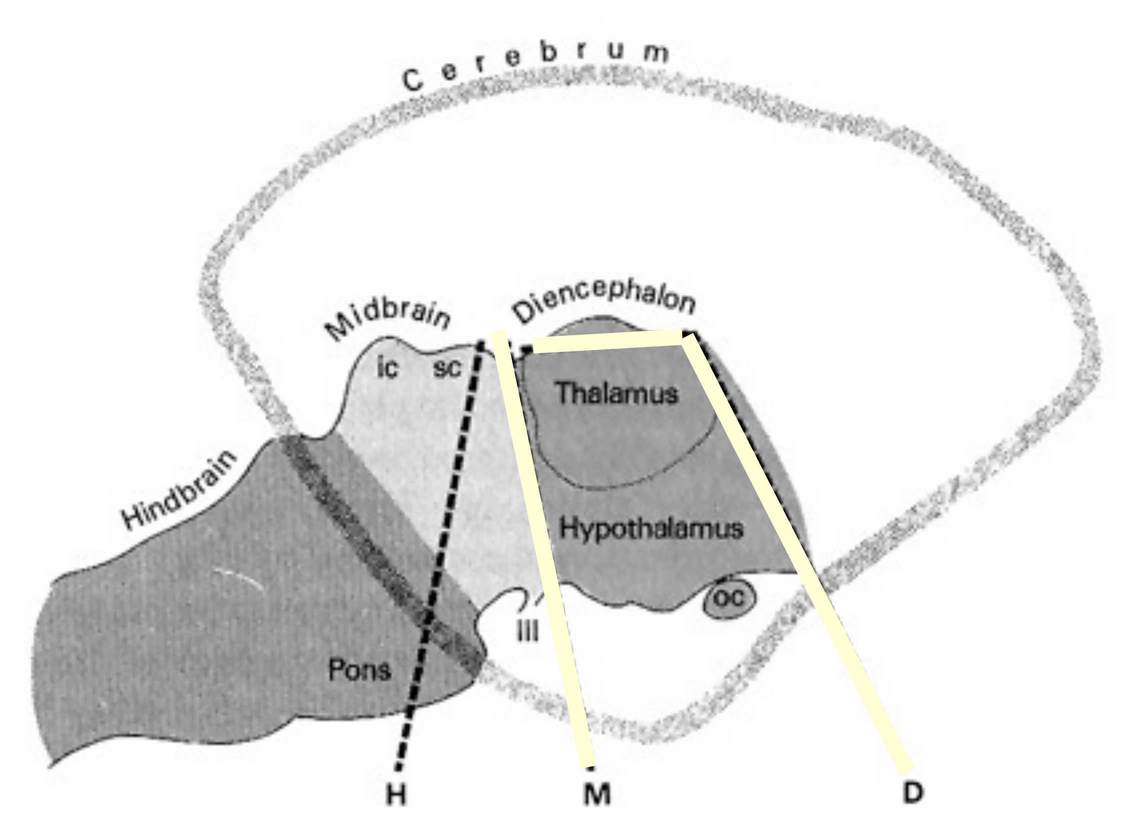
Transection studies

Diencephalic rat—

generates motivated sequences

Midbrain rat—

Capacity for individual actions



Transection studies

Diencephalic rat—

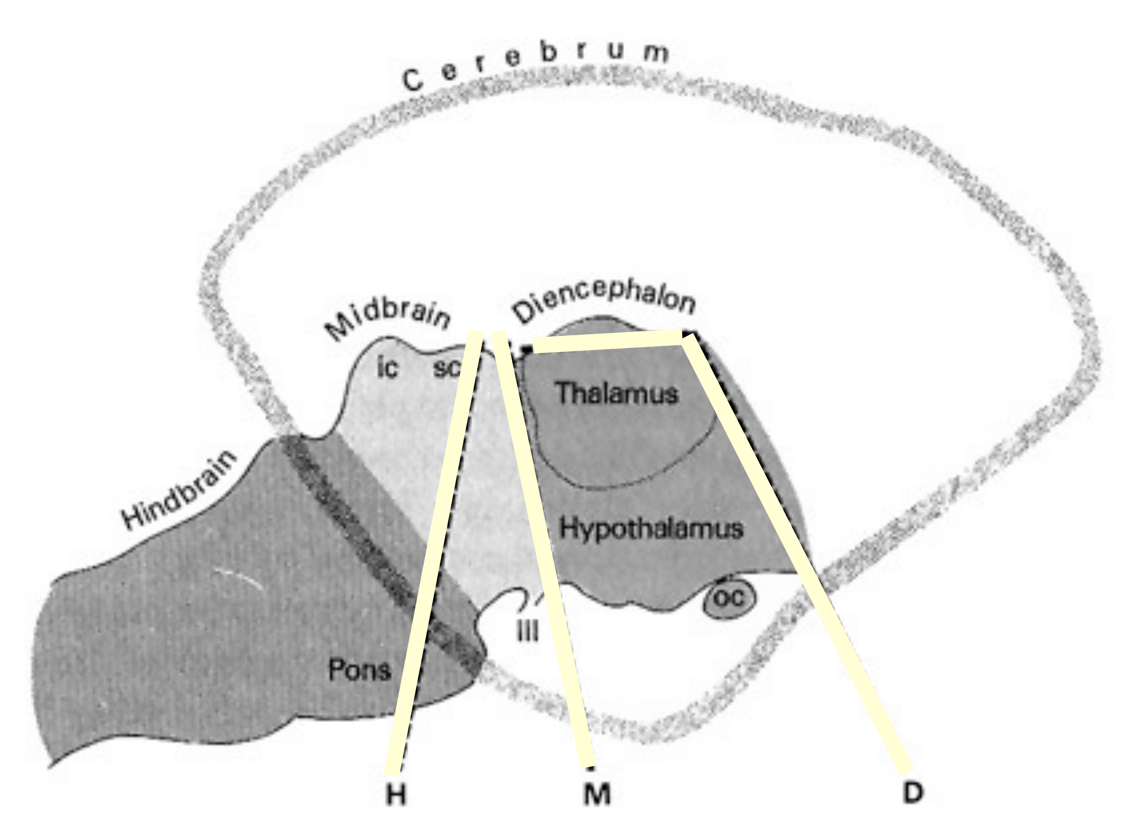
generates motivated sequences

Midbrain rat—

Capacity for individual actions

Hindbrain rat—

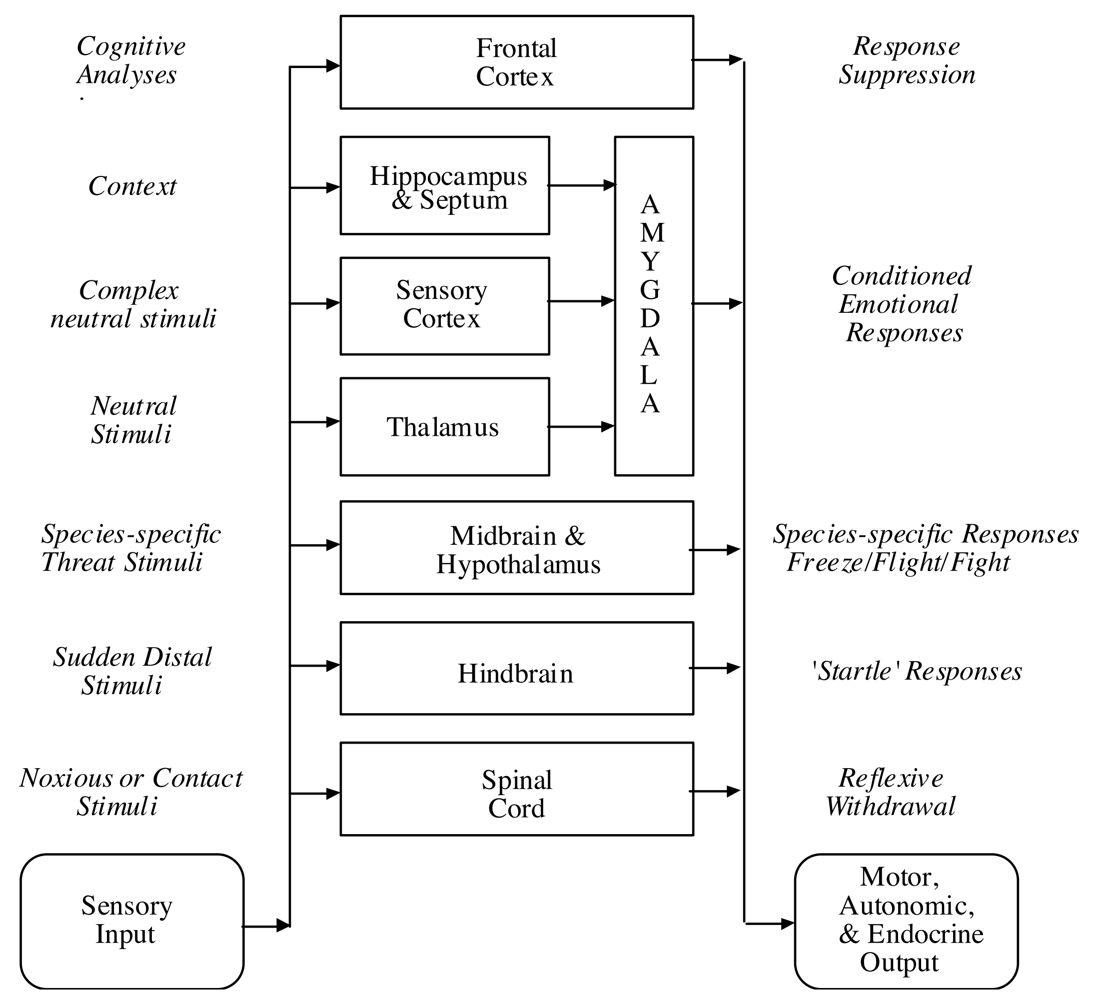
Component movements spared



Layered architecture for defense

The resolution of conflict problems between the different levels of the neuraxis (spinal cord, hind-brain, mid-brain, etc.) may be determined by vertical links

For instance, the vertebrate defense system can be viewed as a set of dissociable layers in which higher levels can suppress or modulate the outputs of lower levels



Cognitive Analyses

Frontal Cortex

Response Suppression

Context

Hippocampus & Septum

AMYGDALA

Complex neutral stimuli

Sensory Cortex

Conditioned Emotional Responses

Neutral Stimuli

Thalamus

Species-specific Threat Stimuli

Midbrain & Hypothalamus

Species-specific Responses Freeze/Flight/Fight

Sudden Distal Stimuli

Hindbrain

'Startle' Responses

Noxious or Contact Stimuli

Spinal Cord

Reflexive Withdrawal

Sensory Input

Motor, Autonomic, & Endocrine Output

Adaptive Behavior 1999, 7(1), 99-127

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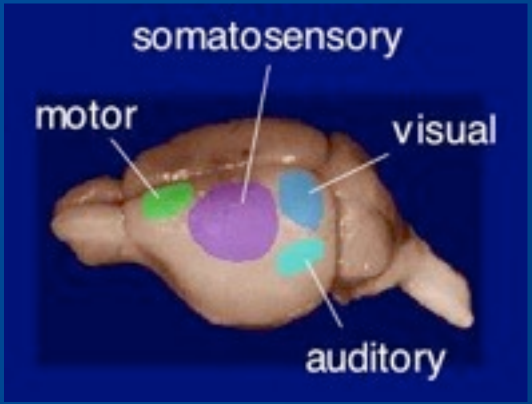
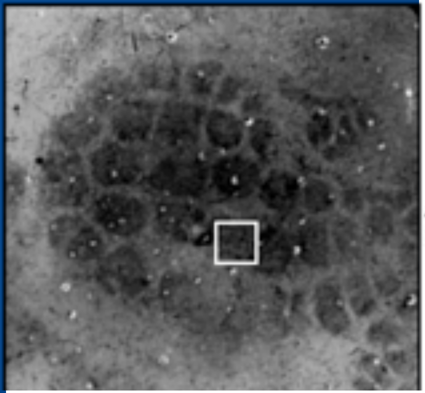
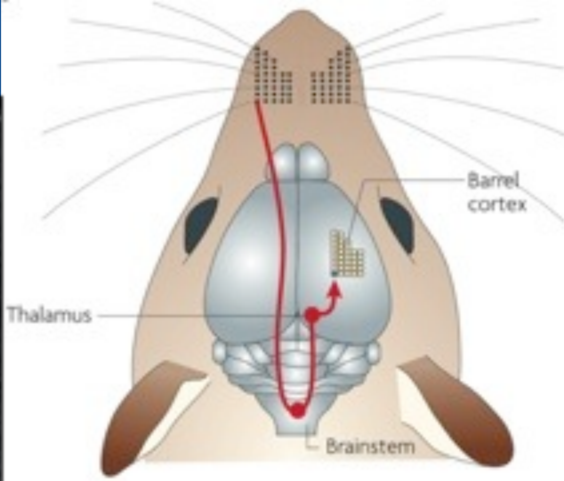
Layered architecture for vibrissal control



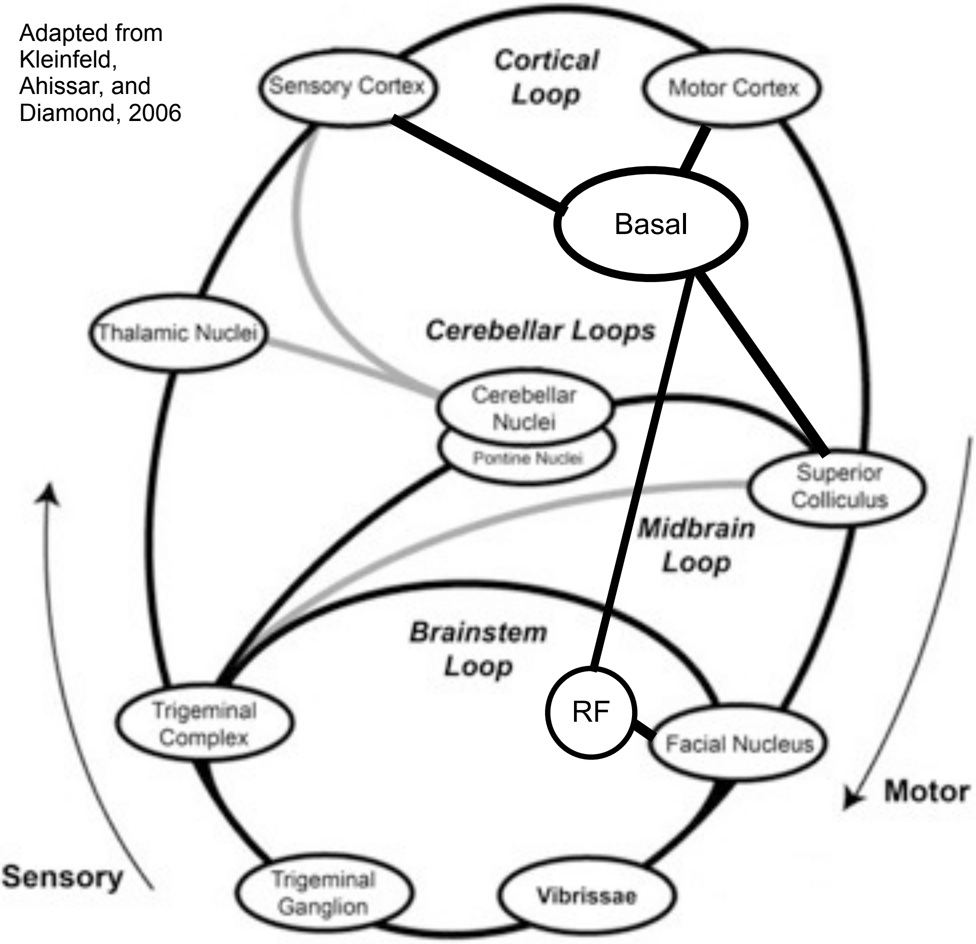
http://www.nibb.ac.jp/brish/Gallery/cortexE.html

From Diamond et al. 2008

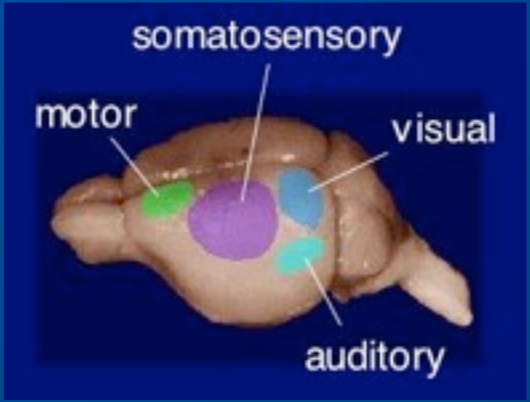




Adapted from Kleinfeld, Ahissar, and Diamond, 2006



Layered architecture for vibrissal control



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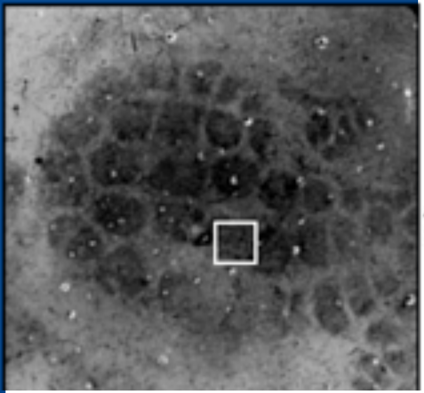

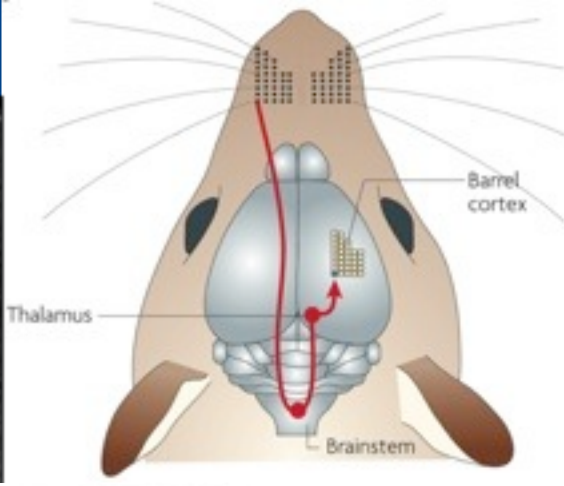

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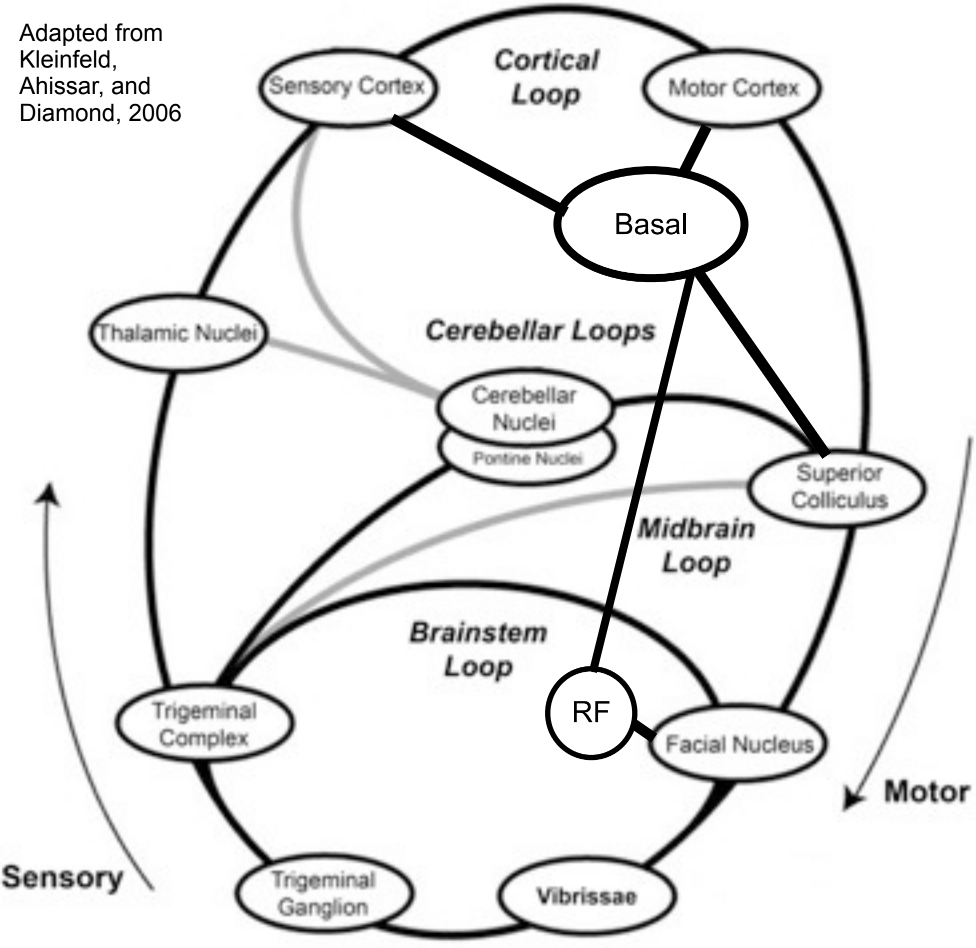
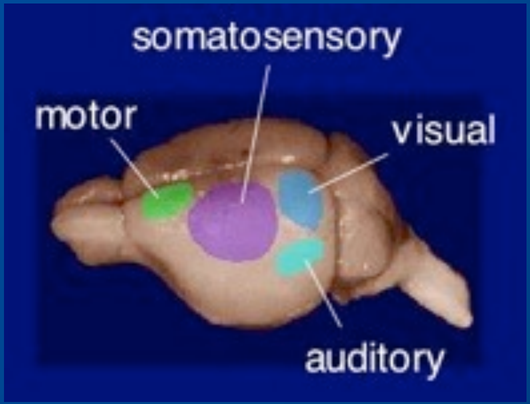


Layered architecture for vibrissal control



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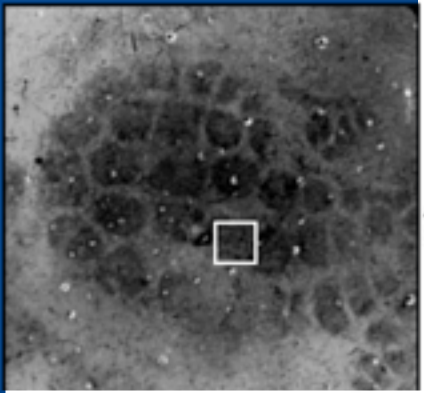

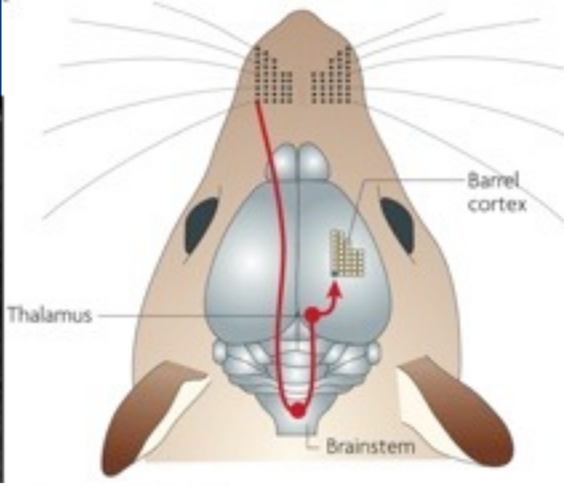

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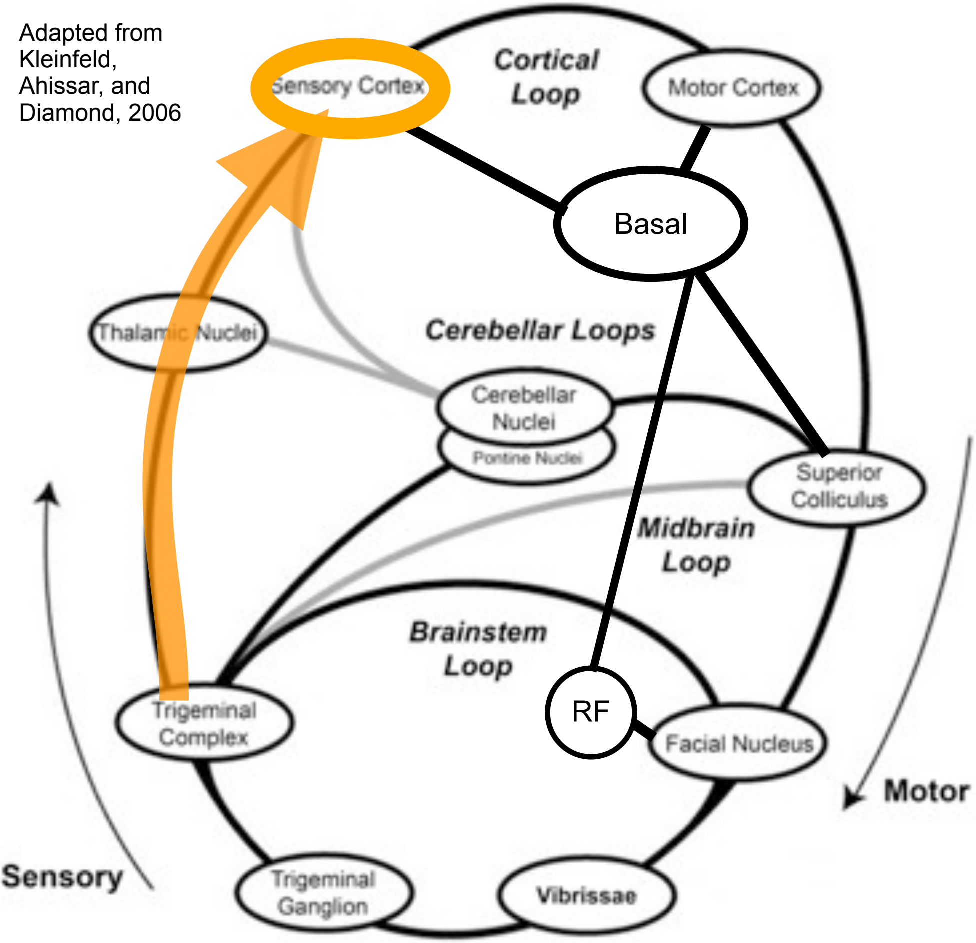
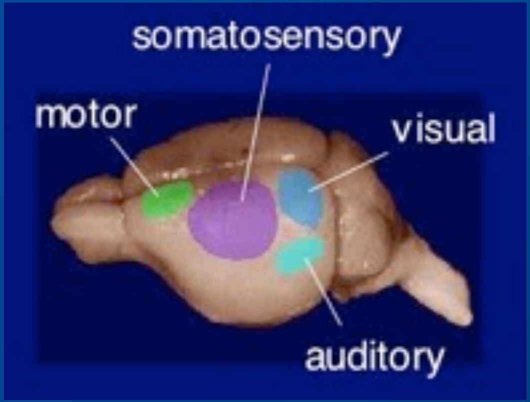


Layered architecture for vibrissal control



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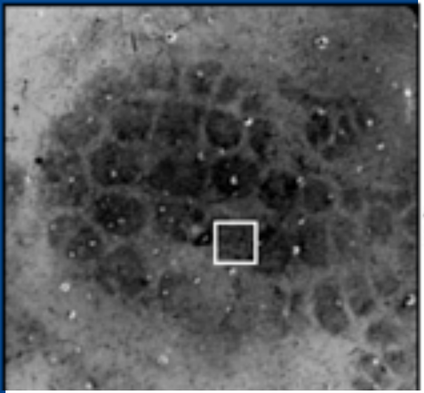

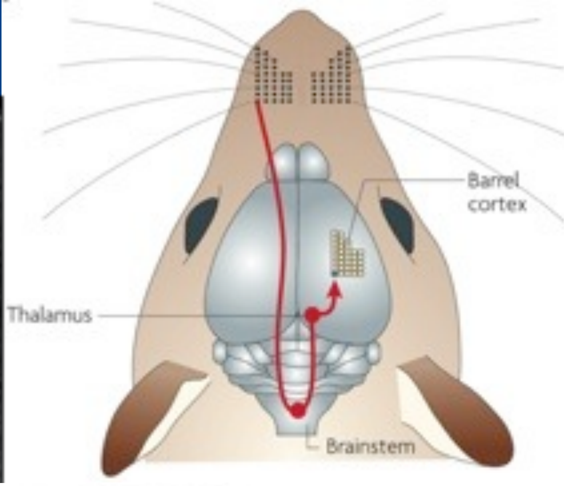

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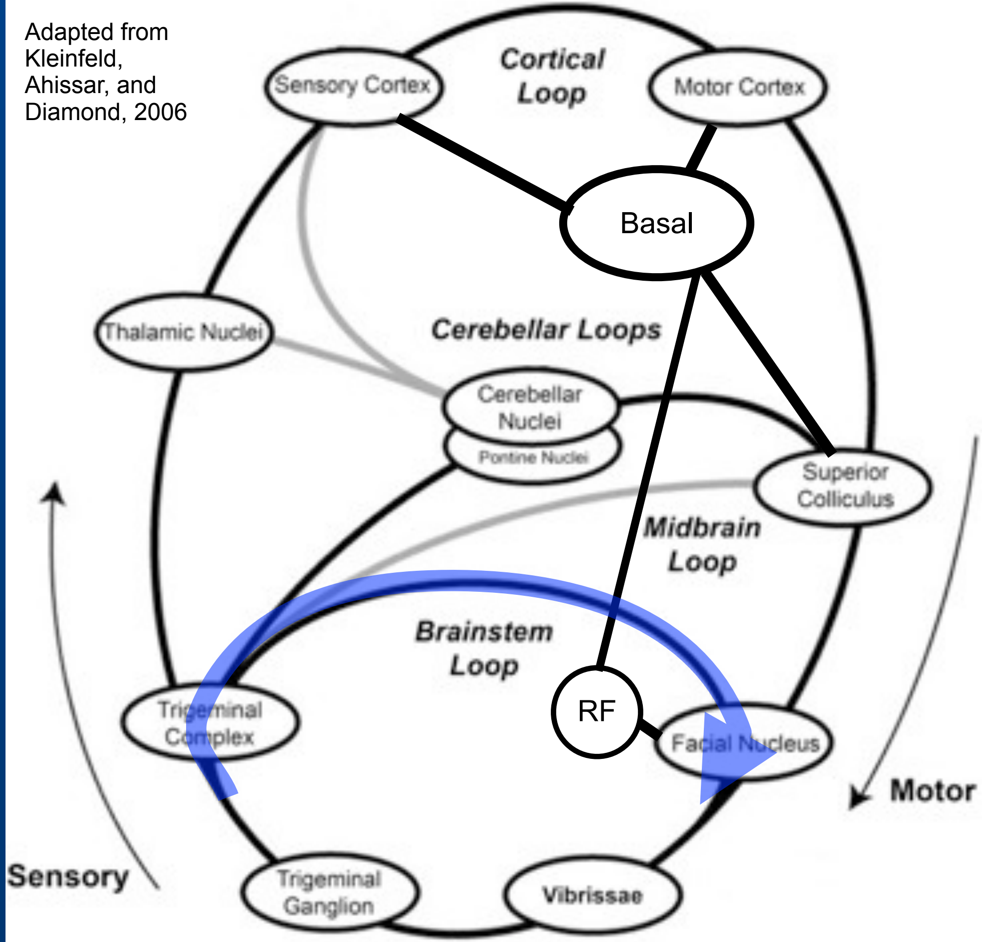

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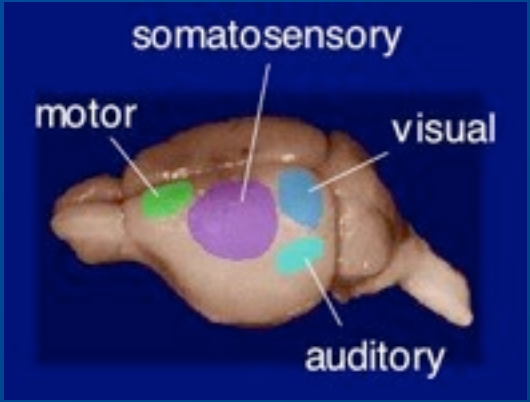

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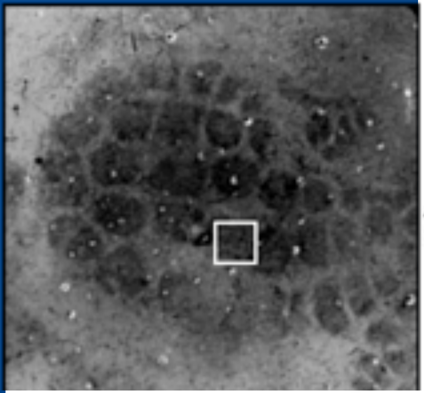

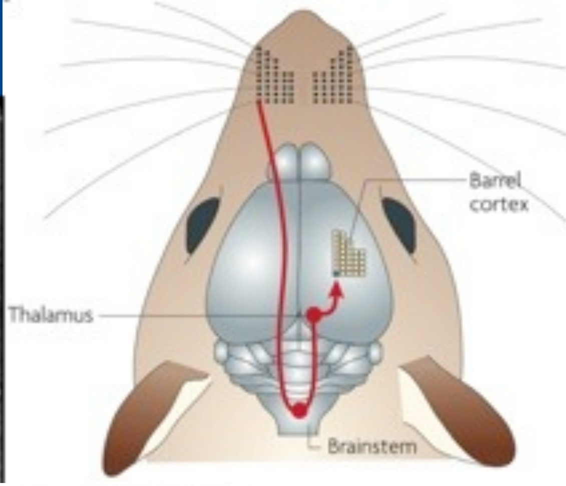

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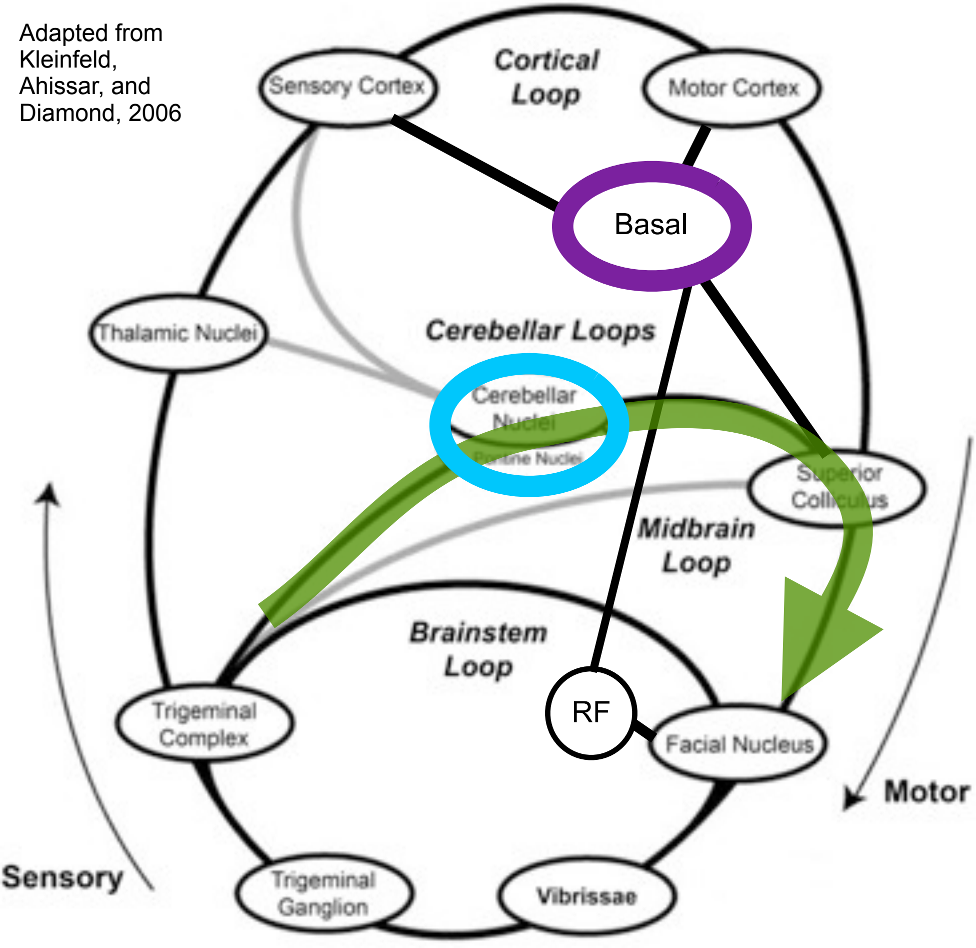
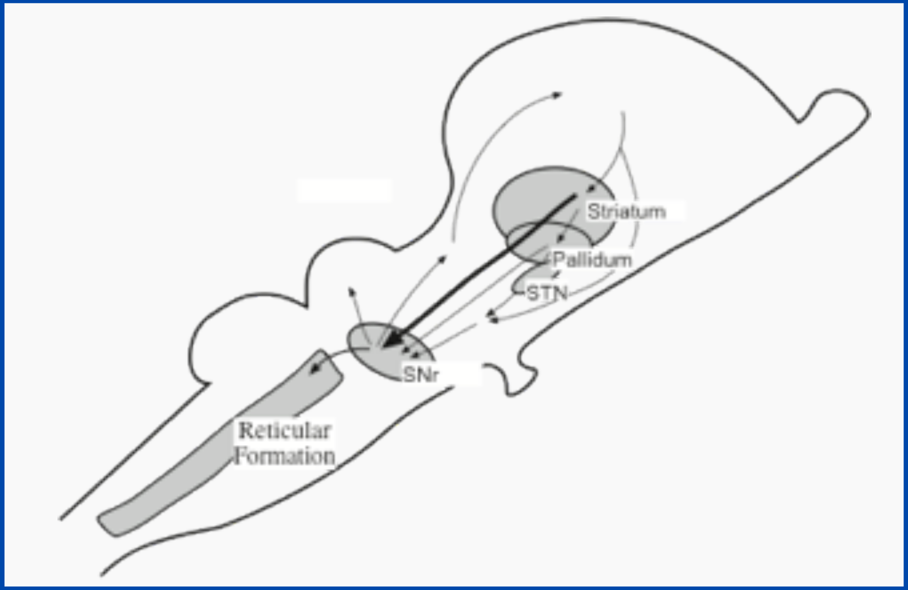
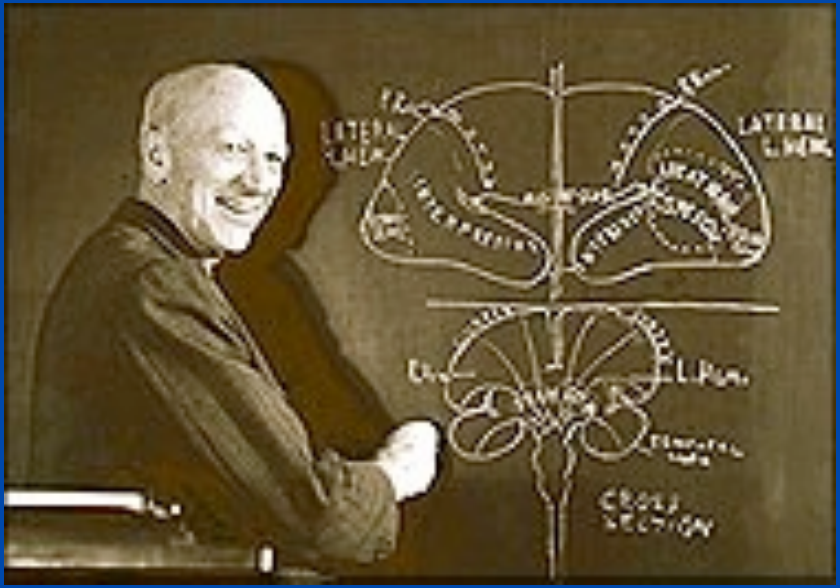


Organising principles II.
A central integrative core

A group of central, sub-cortical brain structures serves to coordinate and integrate the activity of both higher- (cortical) and lower-level neural systems.



This notion is captured in the notion of a *centrencephalic* dimension to nervous system organization



Wilder Penfield
1891-1976

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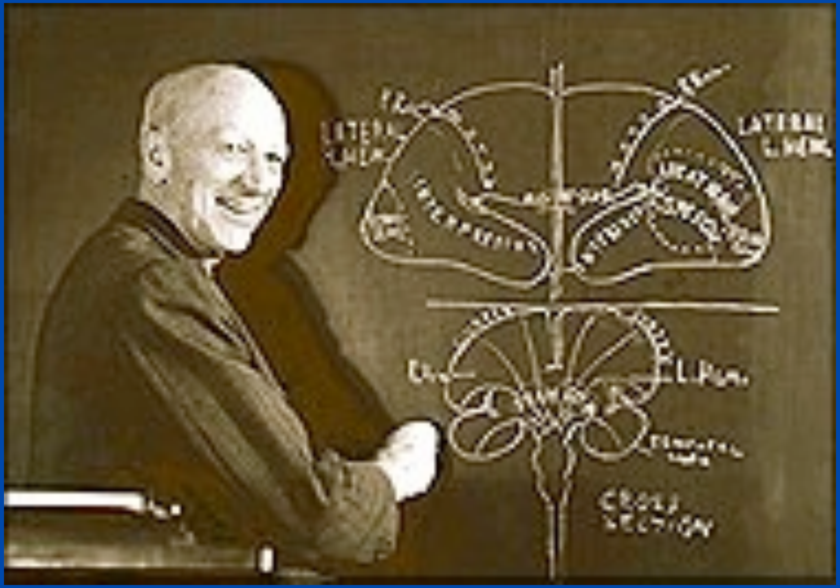

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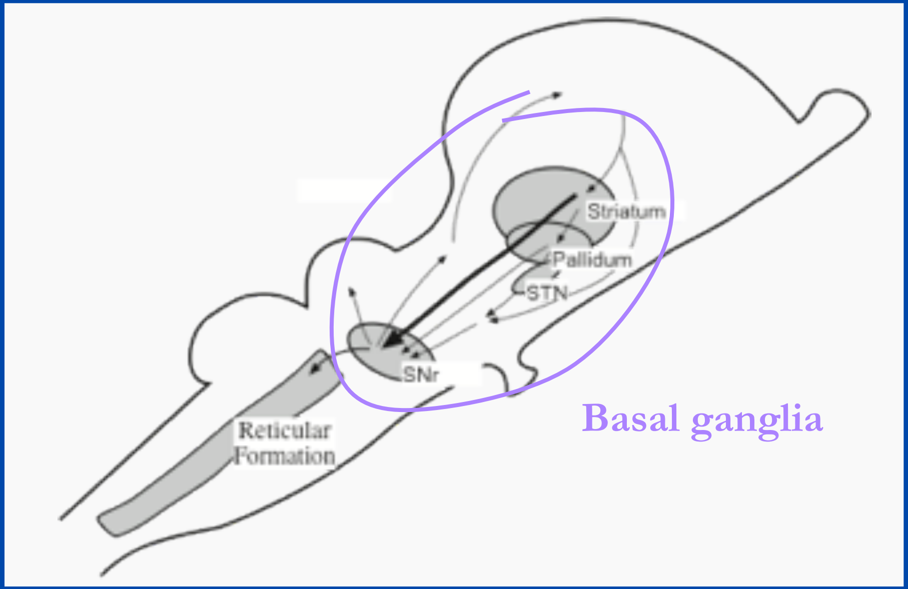

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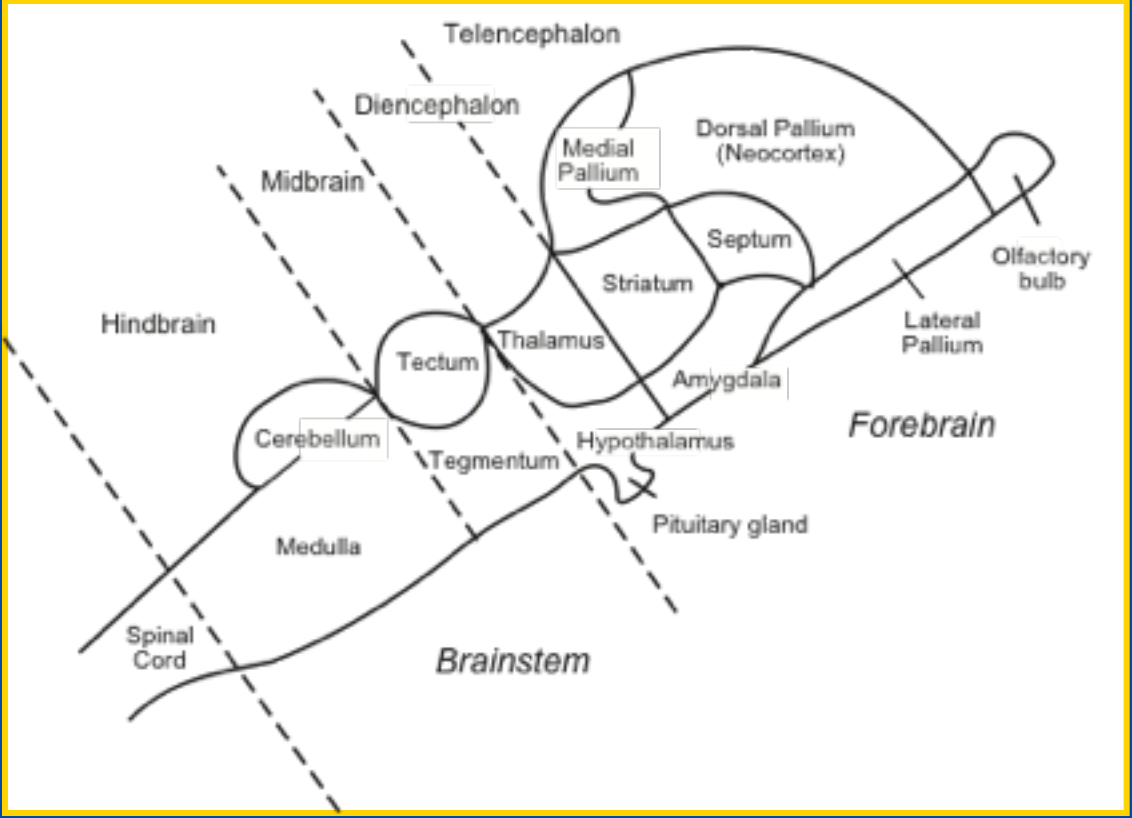
Candidate mechanisms for action selection in the vertebrate brain



Evolutionary neurobiology suggests that a ‘ground plan’ for the nervous system is shared by all vertebrate classes

Candidate action selection mechanisms:

Layered conflict resolution

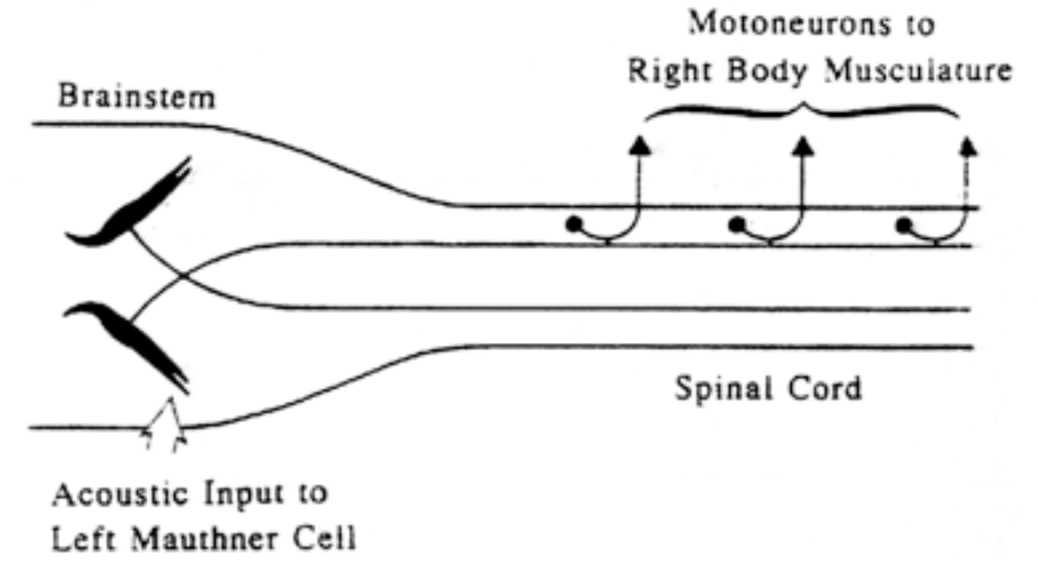
Conflict resolution at the final point of entry to the shared motor resource

Recurrent reciprocal inhibition

Centralised action selection in the basal ganglia and reticular formation

Emergent action selection

Conflict resolution at the final point of entry to the shared motor resource



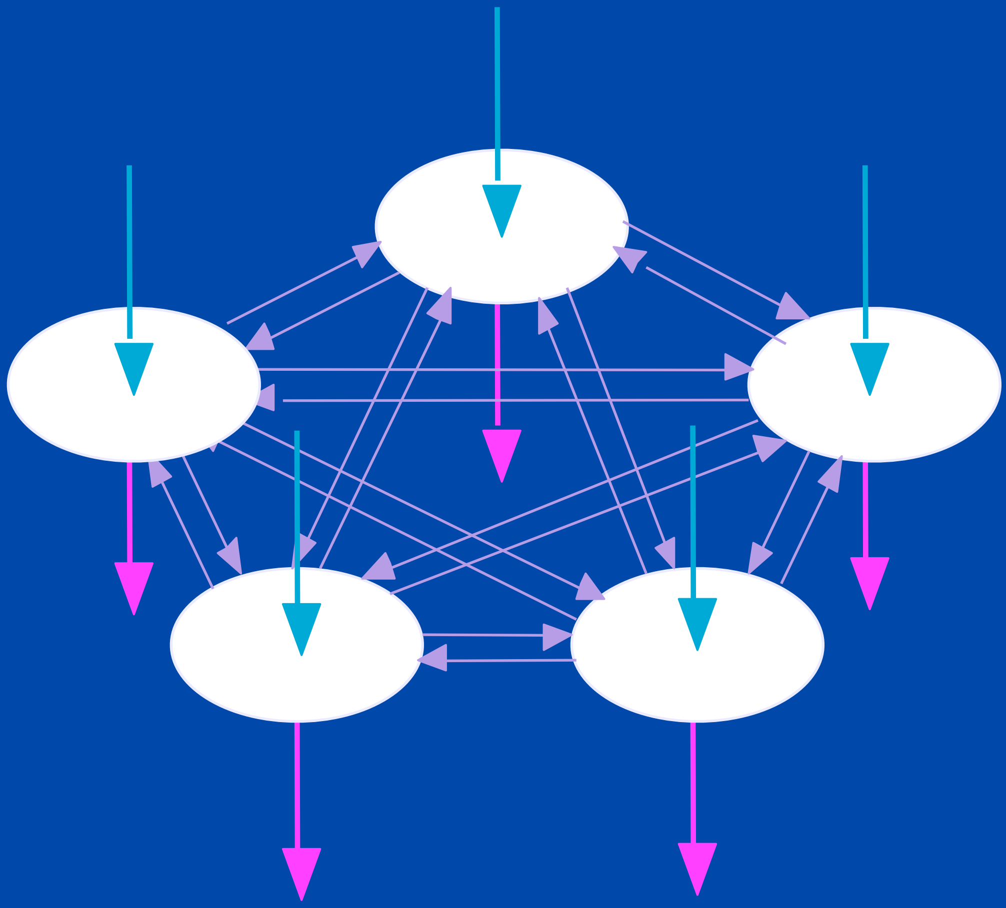
The role of the fish giant Mauthner axon may not be to initiate the C-start but to *suppress competing behaviors*

From Eaton et al., 1995

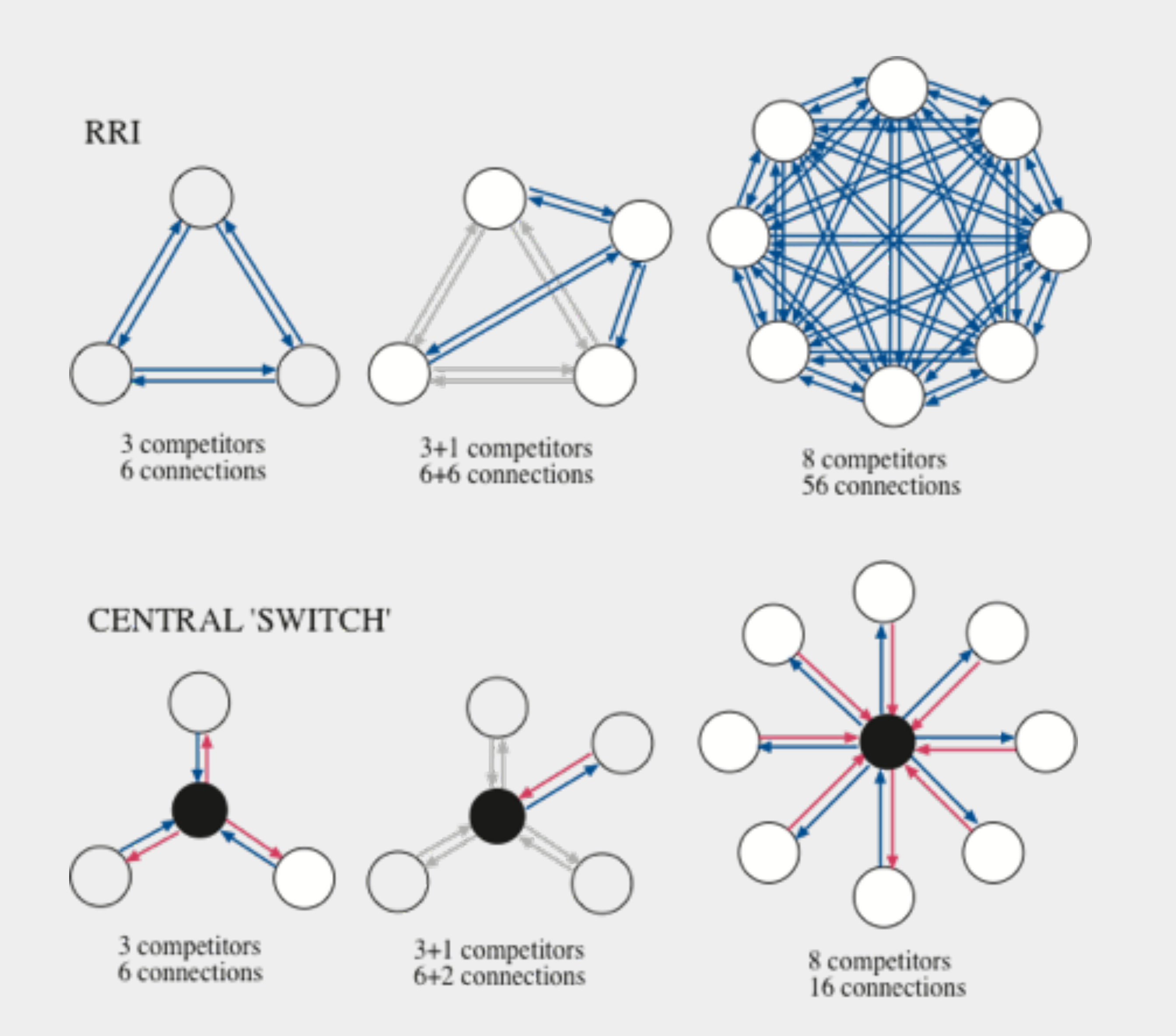
Recurrent reciprocal inhibition

Reciprocal inhibitory connectivity has been identified in many different areas of the vertebrate brain, however, its functional role in most situations is not clearly understood

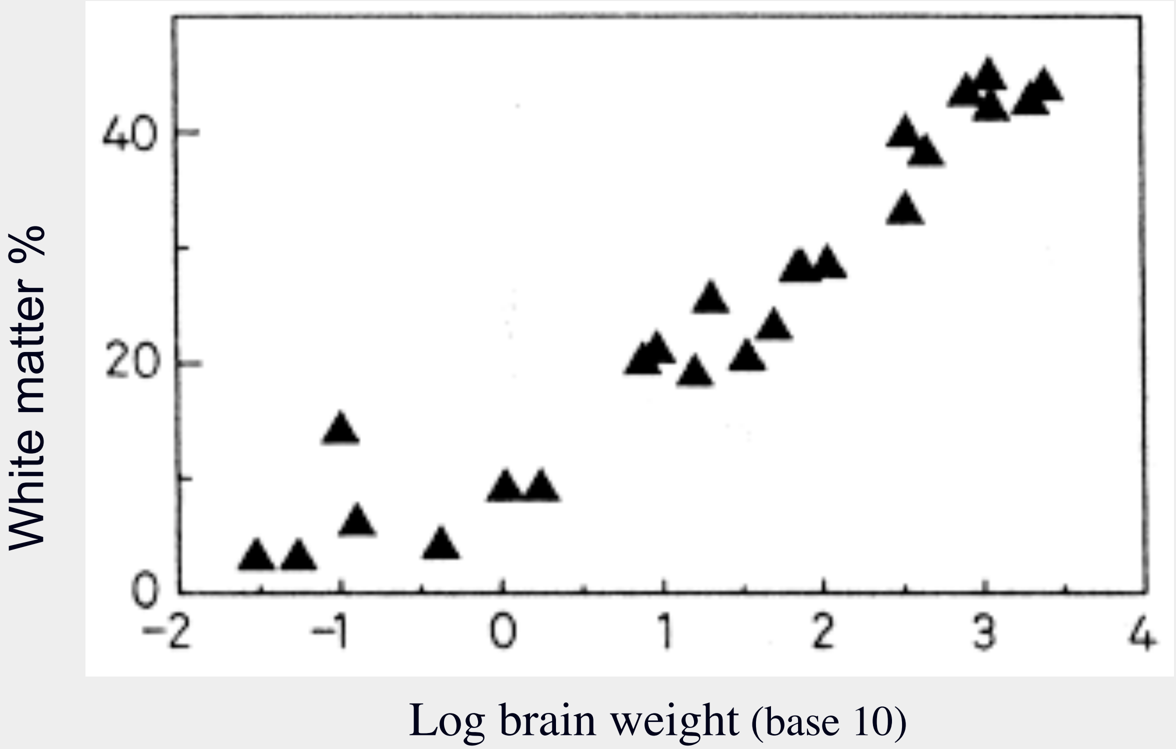
Gallistel has suggested that such circuits could play a role in conflict resolution at multiple levels of the vertebrate nervous system



Centralised action selection mechanisms can scale better



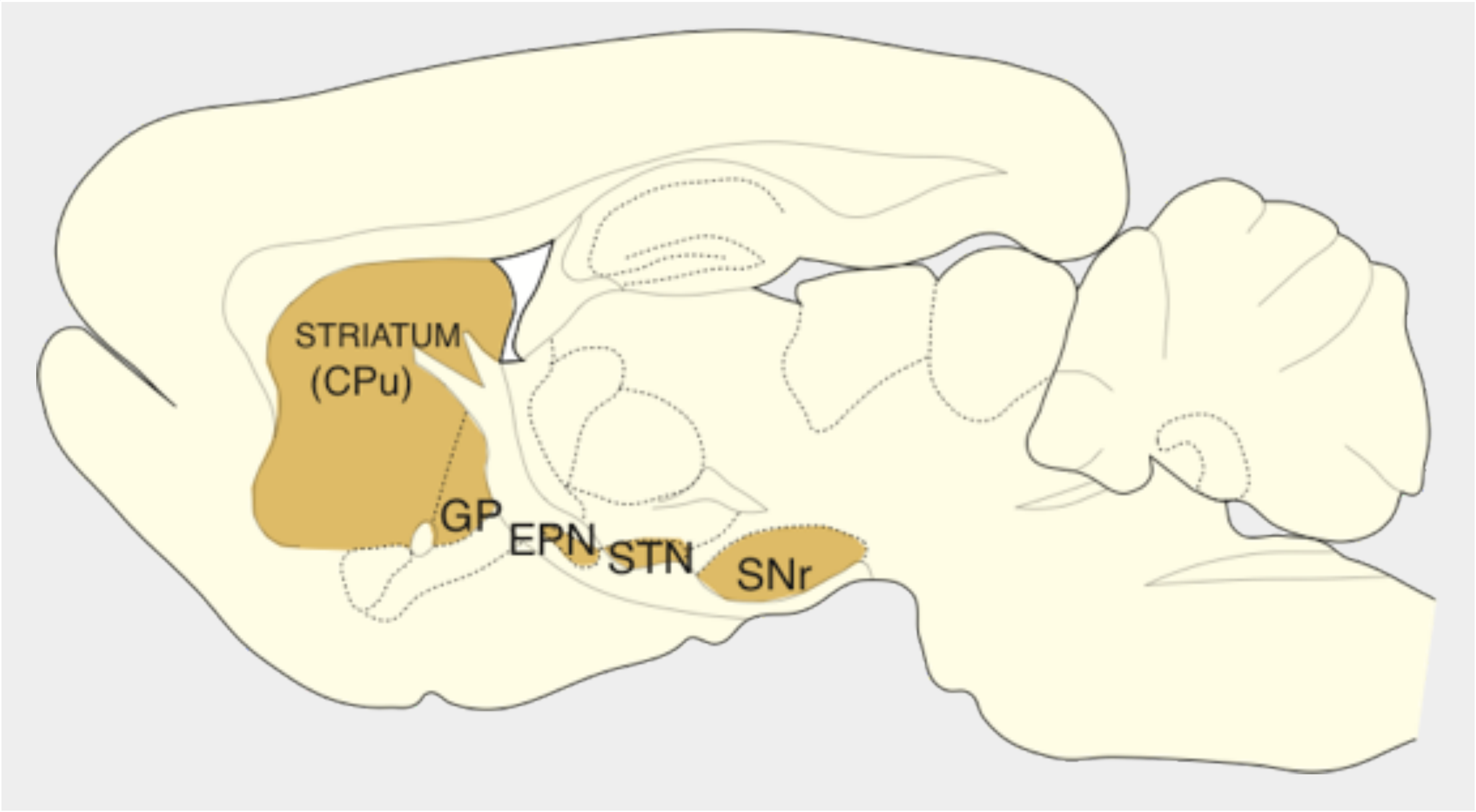
Scaling and brain size

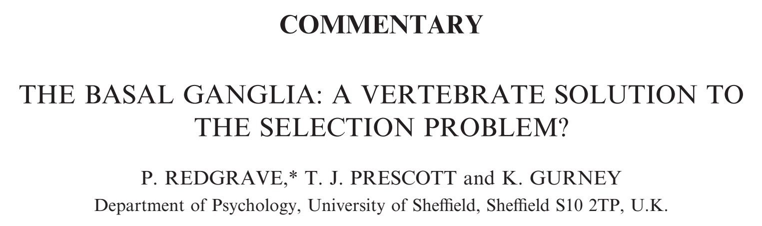


(Graph from Ringo, 1991)

Larger brains cannot support the same degree of connectivity as smaller ones and will “tend to show more specialisation” (Ringo, 1991)

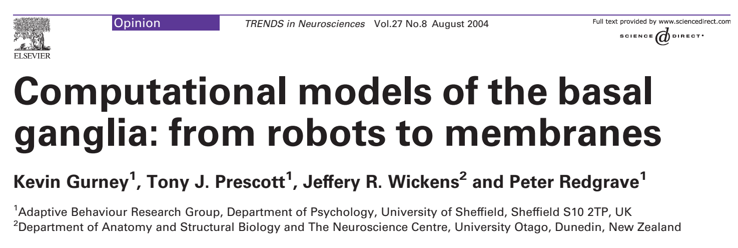
Hypothesis: the vertebrate basal ganglia—a specialised action selection mechanism




COMMENTARY

THE BASAL GANGLIA: A VERTEBRATE SOLUTION TO
THE SELECTION PROBLEM?

P. REDGRAVE,* T. J. PRESCOTT and K. GURNEY
Department of Psychology, University of Sheffield, Sheffield S10 2TP, U.K.


Opinion *TRENDS in Neurosciences* Vol.27 No.8 August 2004

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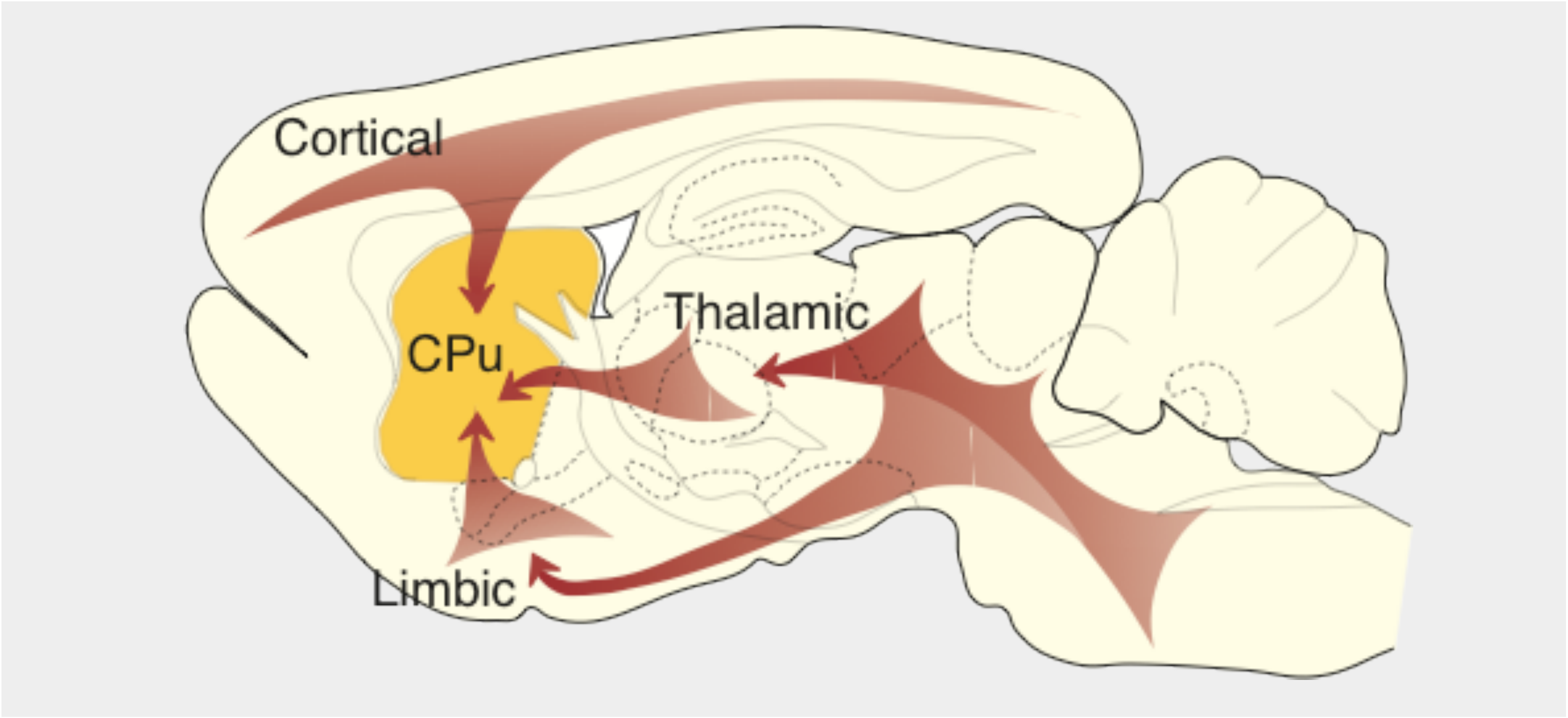
Computational models of the basal ganglia: from robots to membranes

Kevin Gurney[1], Tony J. Prescott[1], Jeffery R. Wickens[2] and Peter Redgrave[1]

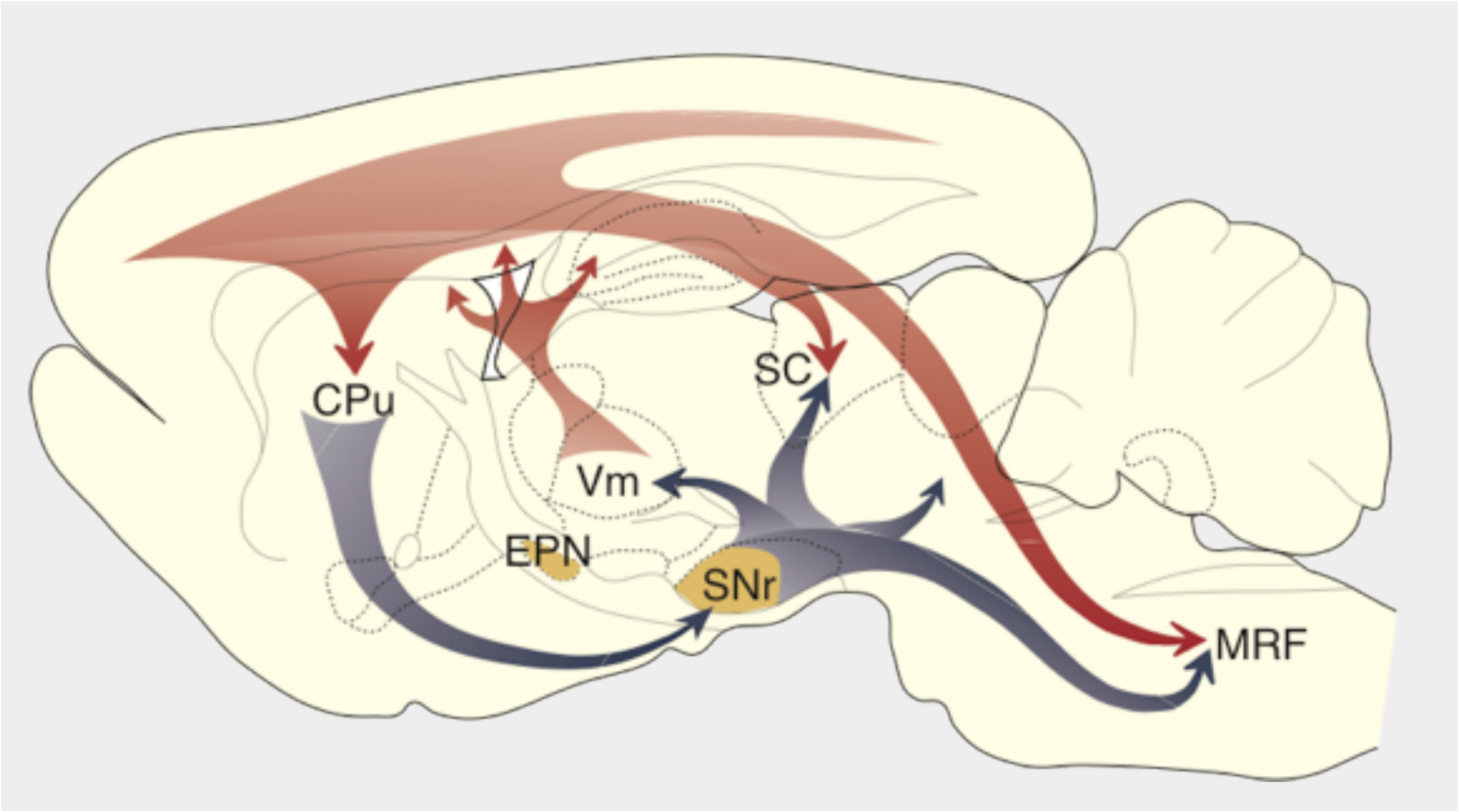
[1]Adaptive Behaviour Research Group, Department of Psychology, University of Sheffield, Sheffield S10 2TP, UK
[2]Department of Anatomy and Structural Biology and The Neuroscience Centre, University Otago, Dunedin, New Zealand

Basal ganglia input—
branched pathways from sensorimotor systems



Functional systems specifying action are widely distribute throughout the neuraxis. The striatum receives input from most of the cortex, the limbic system, and motor areas of the brainstem

Basal ganglia output—
disinhibitory control over movement generators

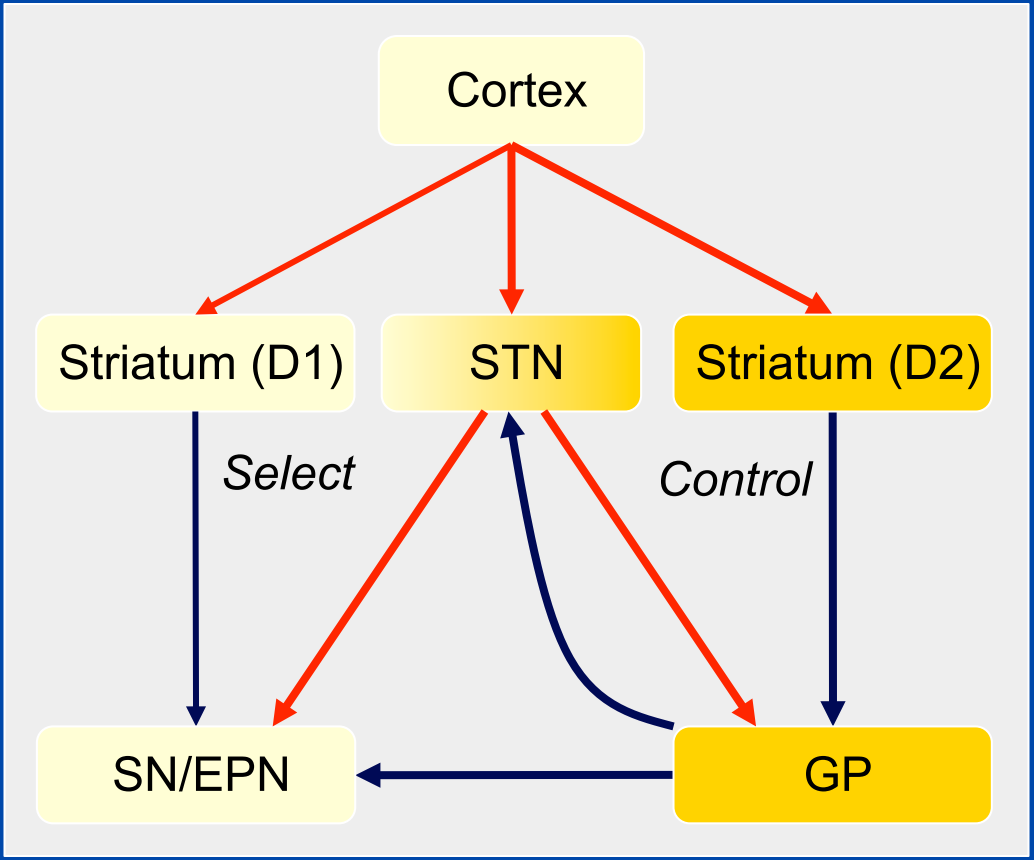


Main *output* centers are *tonically active* and direct a continuous flow of *inhibition* at centers throughout the brain that directly or indirectly generate movement

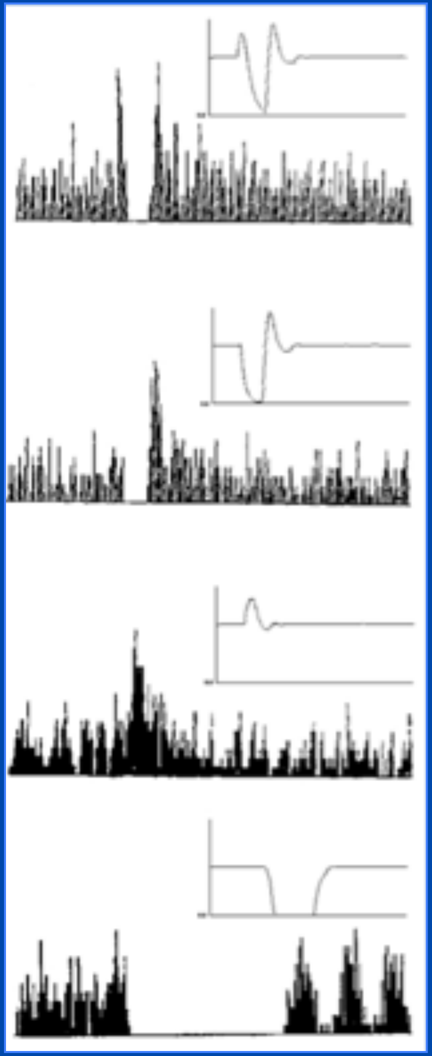
Computational models at the systems level

We have developed (Gurney et al, 1998) a computational model of the basal ganglia viewed as two functional subsystems — a selection subsystem and a control subsystem.

Cell populations are modelled as leaky integrators with piecewise linear output



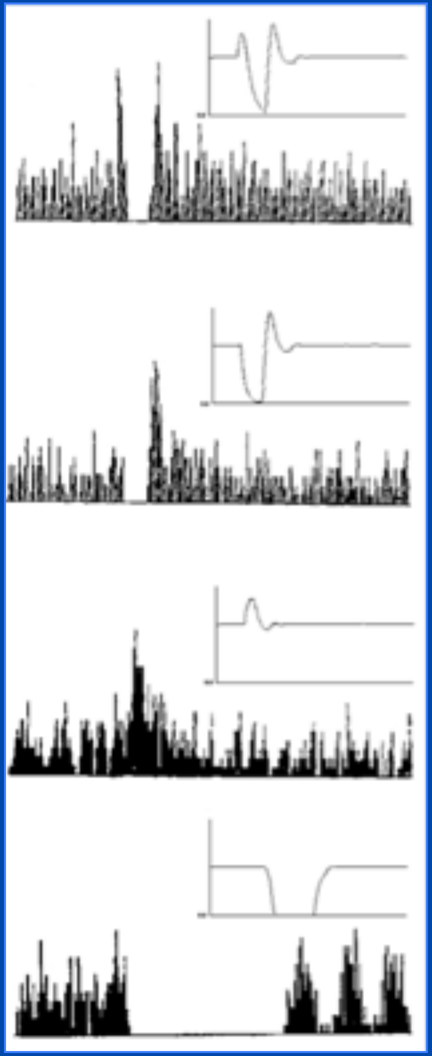
Modelling electrophysiological data



Ryan & Clark (1991) recorded from rat GP following cortical stimulation. The insets show model GP activity with similar patterns of excitatory and inhibitory transients.

traces show histograms of neuronal firing recorded from a single electrode

Modelling electrophysiological data

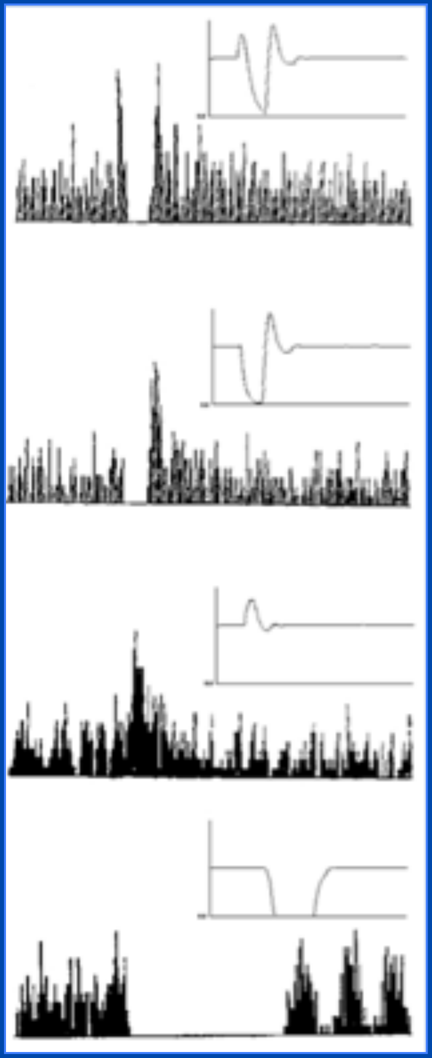


Ryan & Clark (1991) recorded from rat GP following cortical stimulation. The insets show model GP activity with similar patterns of excitatory and inhibitory transients.

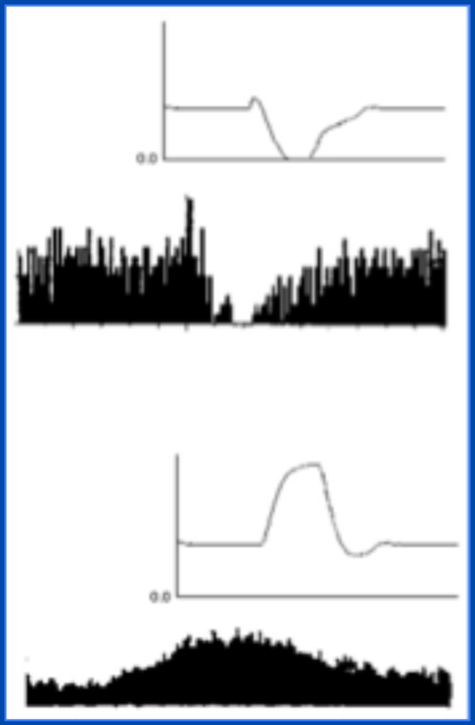
Following lesion of
excitatory input
from STN

traces show histograms of neuronal firing recorded from a single electrode

Modelling electrophysiological data



Ryan & Clark (1991) recorded from rat GP following cortical stimulation. The insets show model GP activity with similar patterns of excitatory and inhibitory transients.



Schultz (1986) recorded from monkey SNr during a behavioural task.

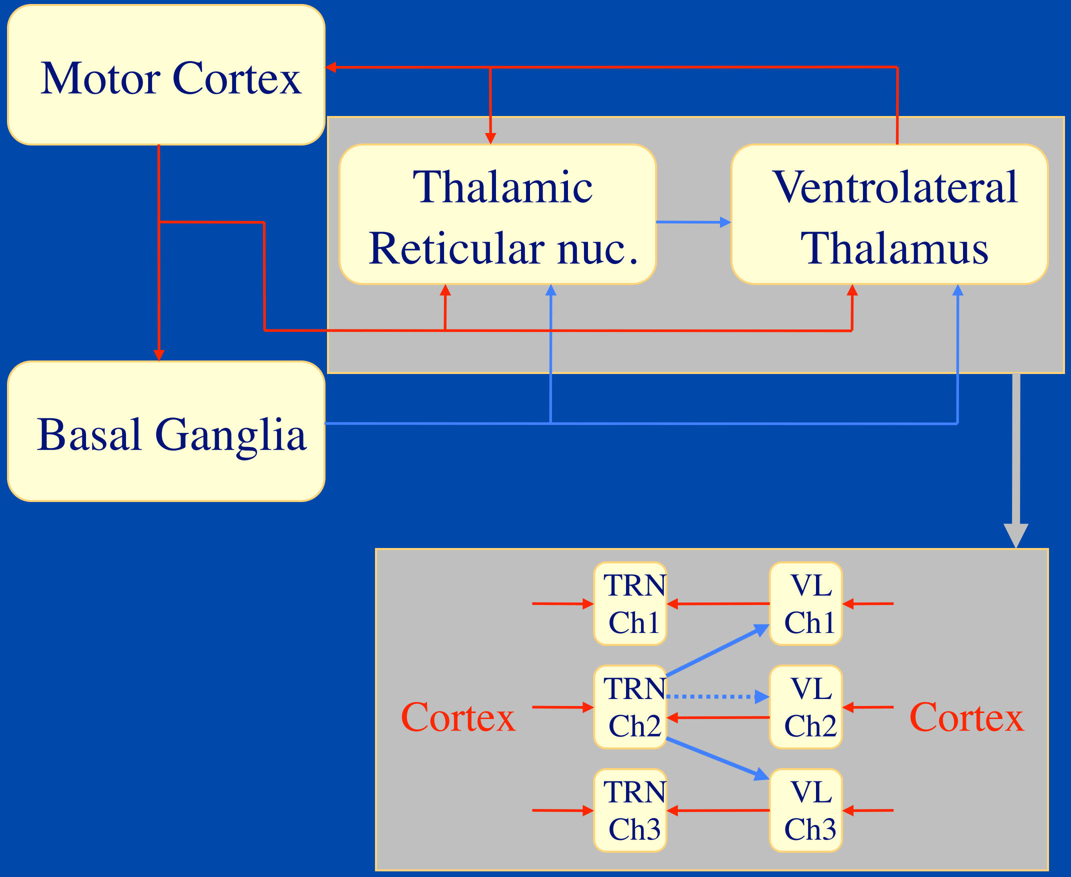
The upper panel shows stimulated (winning) channel, lower panel unstimulated (losing) channel.

traces show histograms of neuronal firing recorded from a single electrode

Including thalamic feedback loops

Humphries and Gurney et al, *Neural Networks, 2002*

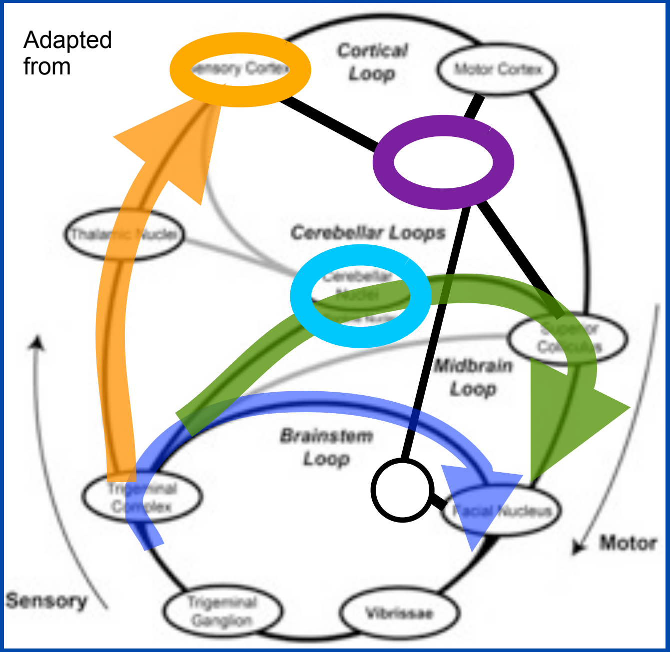
- Added circuits:

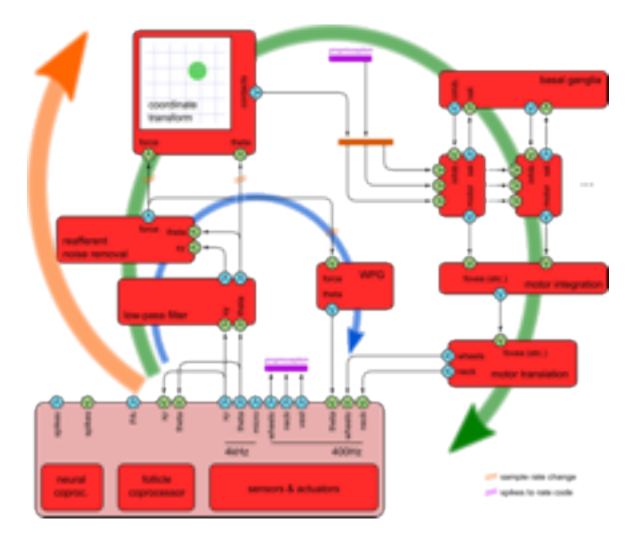


Effects

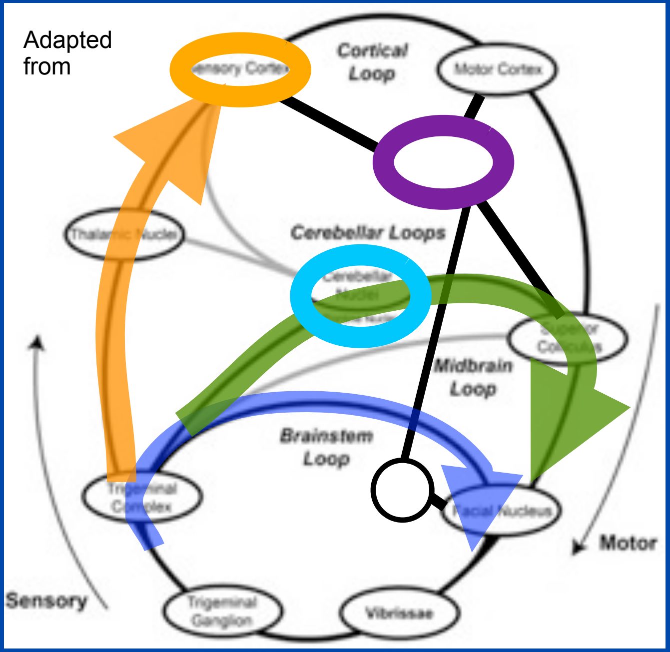
Selection and switching maintained
Reduced distortion
Enhanced selection contrast
Greater dynamic range
Cleaner switching

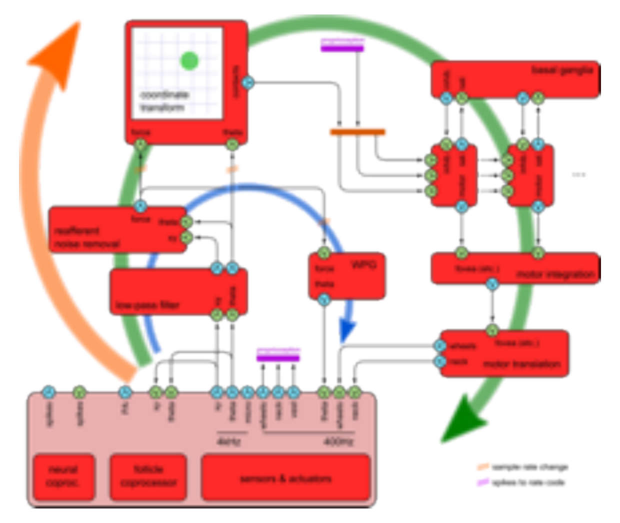
Embedded in robots

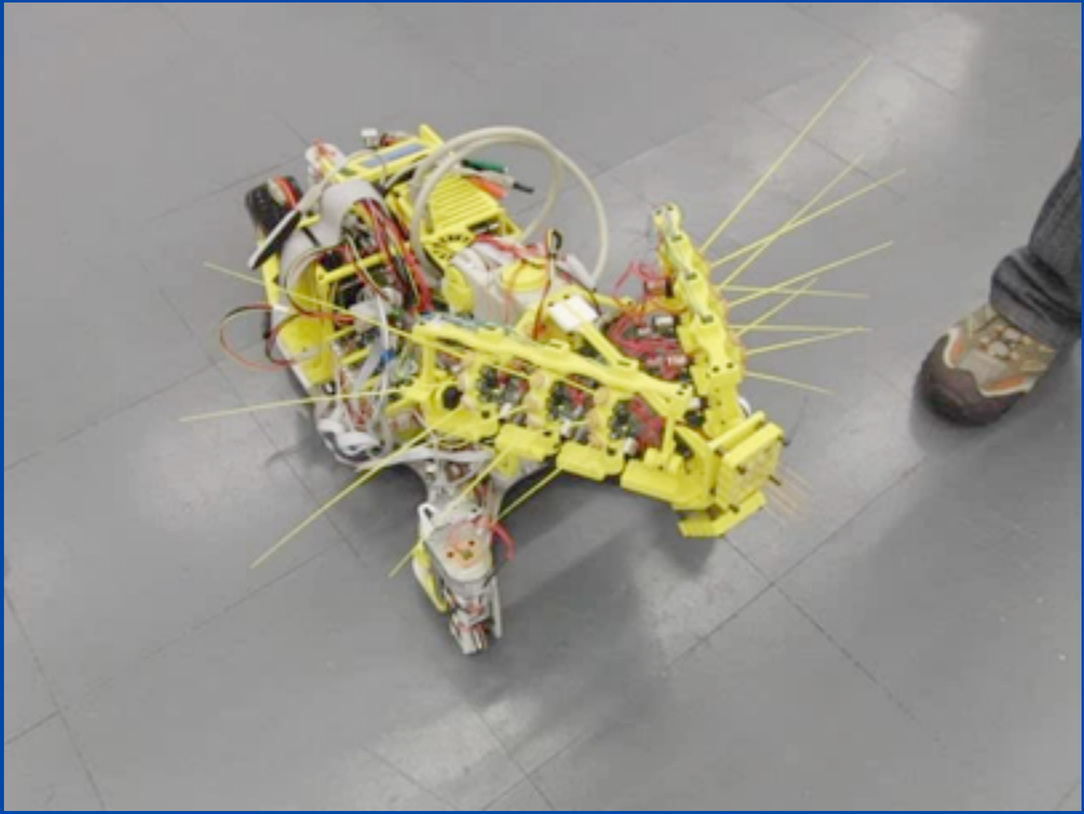

Adapted from



Embedded in robots





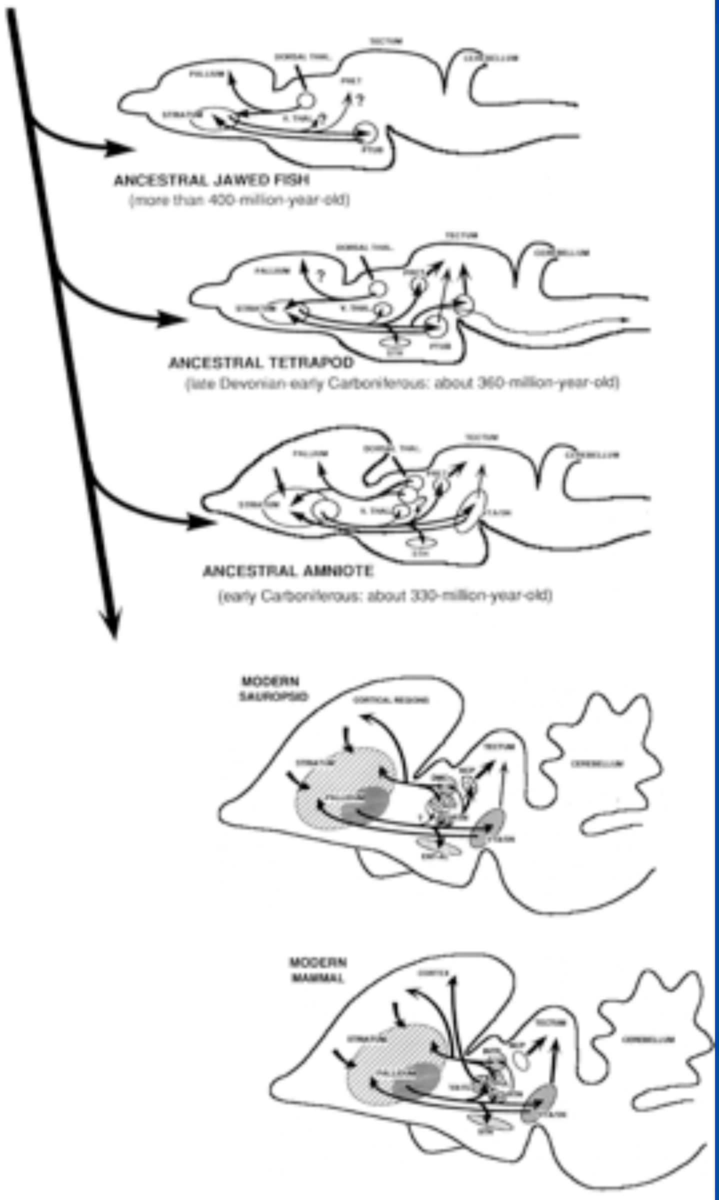


The evolution of the basal ganglia

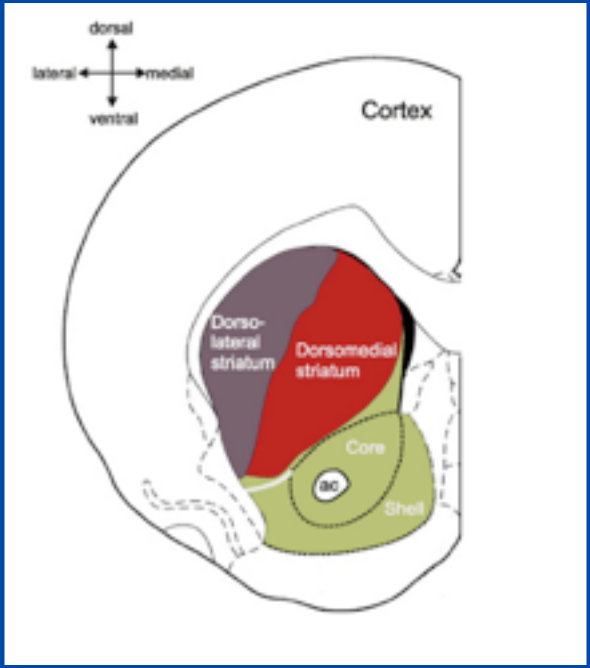
The main basal ganglia nuclei (or homologous nuclei) are found in the nervous systems of all classes of jawed vertebrates and possibly in all vertebrates.

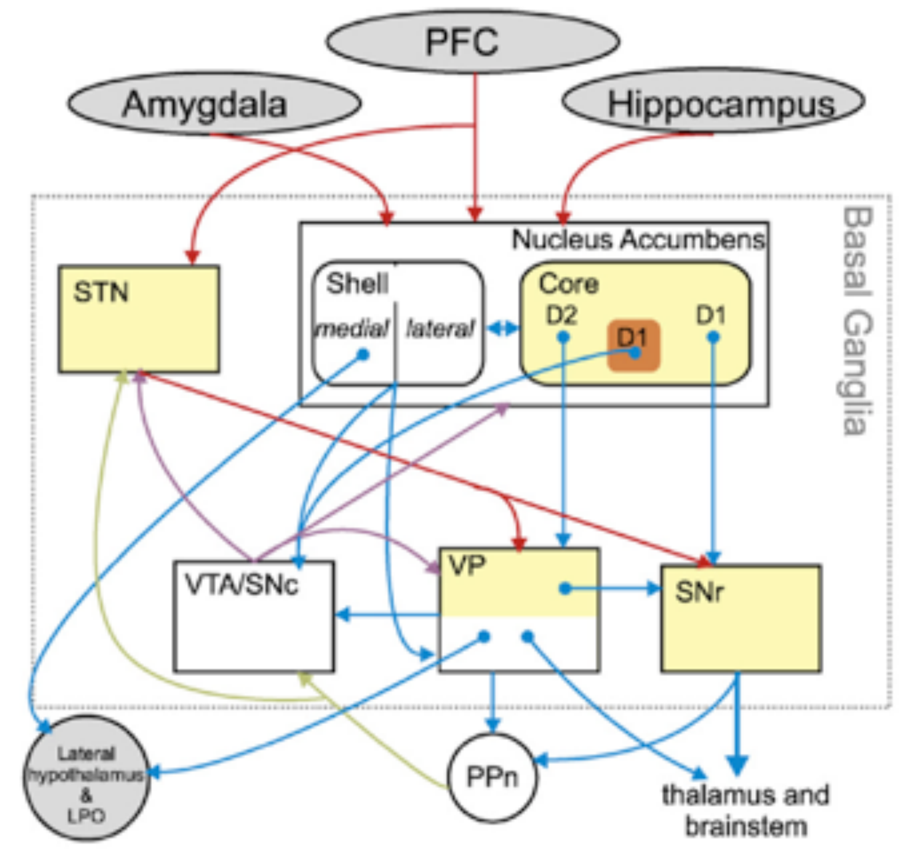
The striatum, in particular, is a substantial structure in all vertebrate brains and occupies a roughly similar proportion of forebrain volume in all the vertebrate classes (Hodos, 1982).

From Medina & Reiner, '95

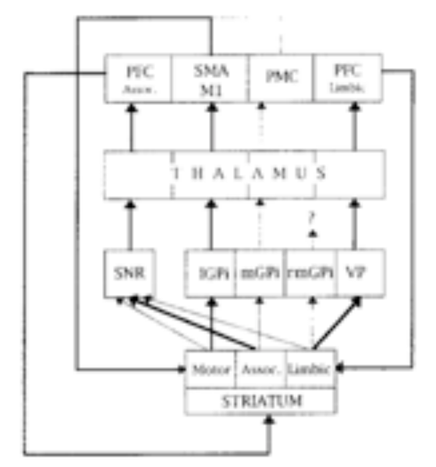


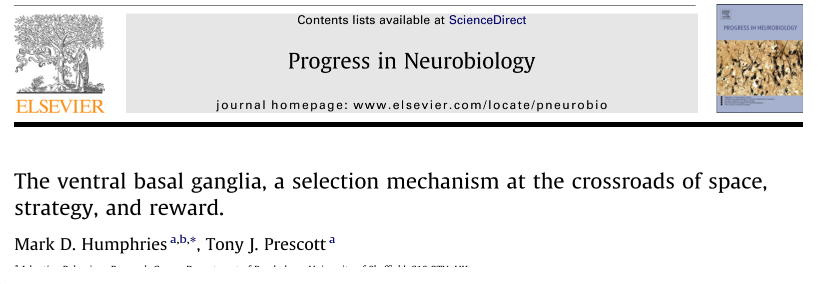
Striatal domains





Joel & Wiener
1999

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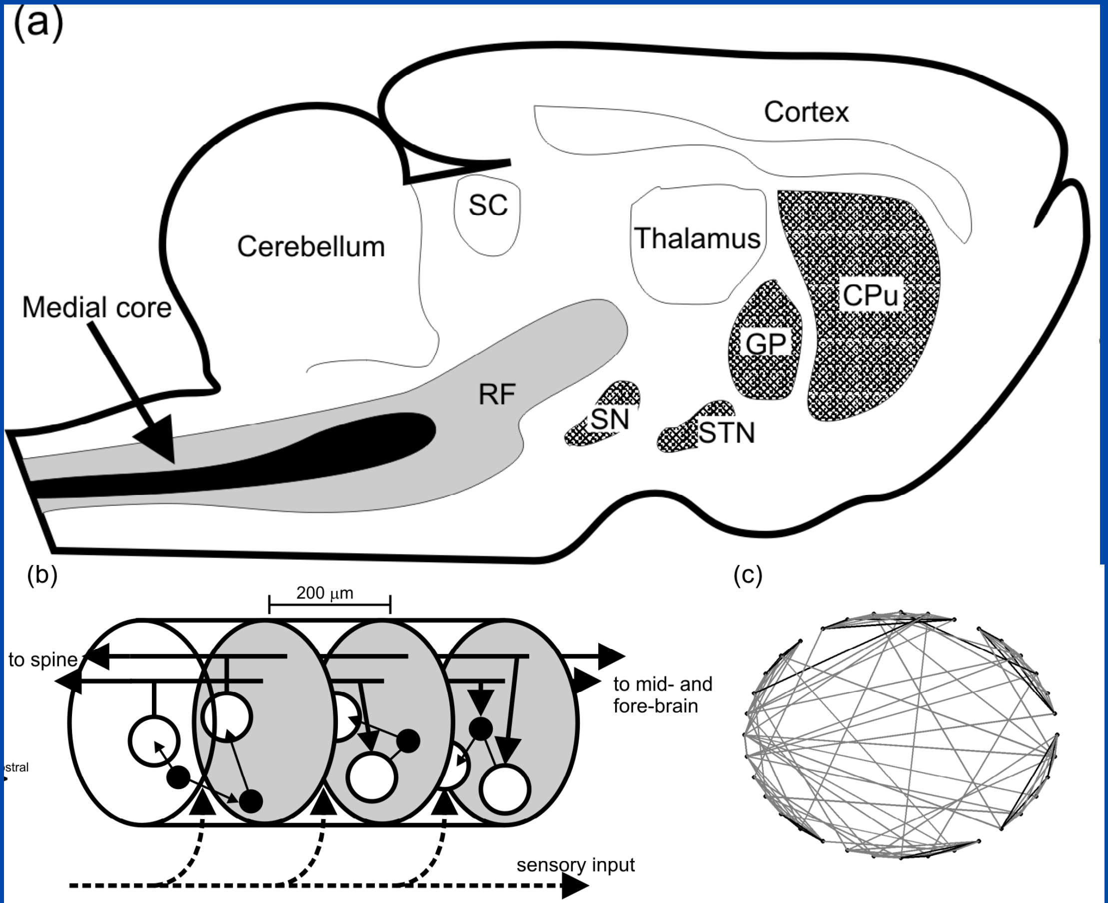
ELSEVIER

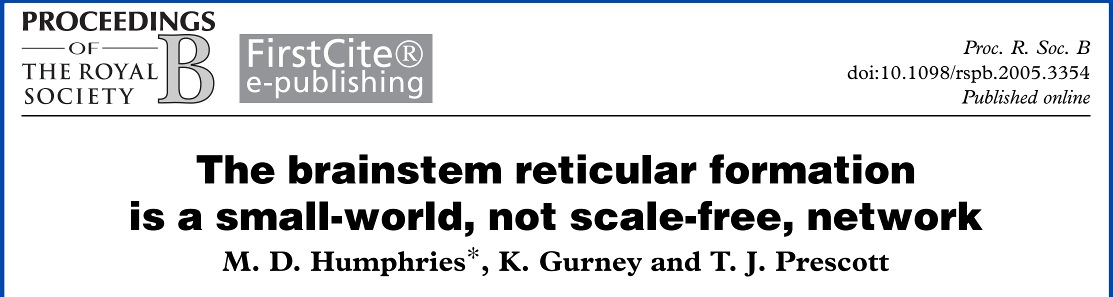
The ventral basal ganglia, a selection mechanism at the crossroads of space, strategy, and reward.

Mark D. Humphries [a,b,*], Tony J. Prescott [a]

The reticular formation

A brainstem substrate for behavioural integration?

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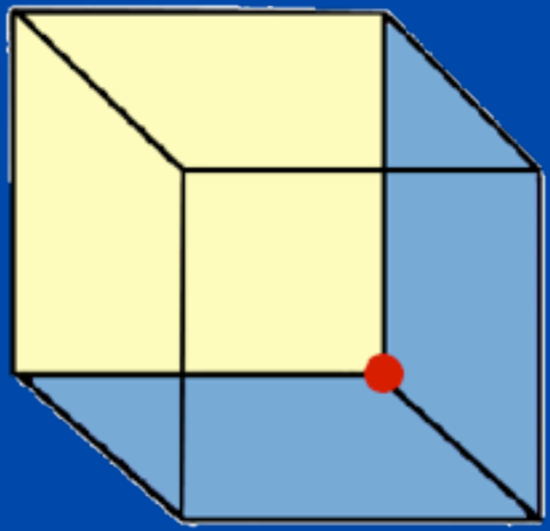
doi:10.1098/rspb.2005.3354

The brainstem reticular formation
is a small-world, not scale-free, network

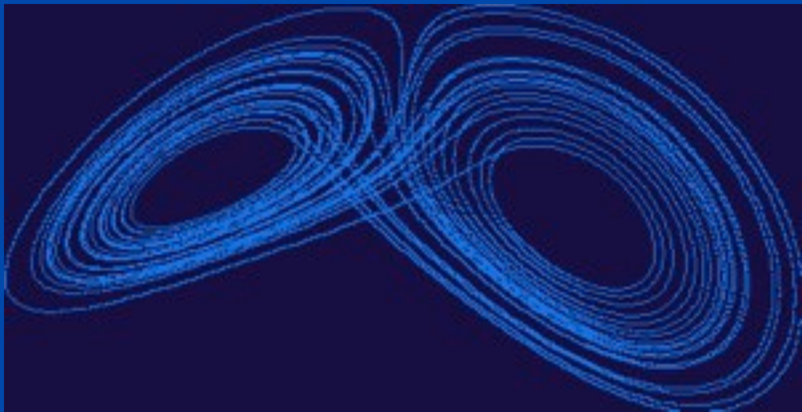
M. D. Humphries*, K. Gurney and T. J. Prescott

Emergent action selection



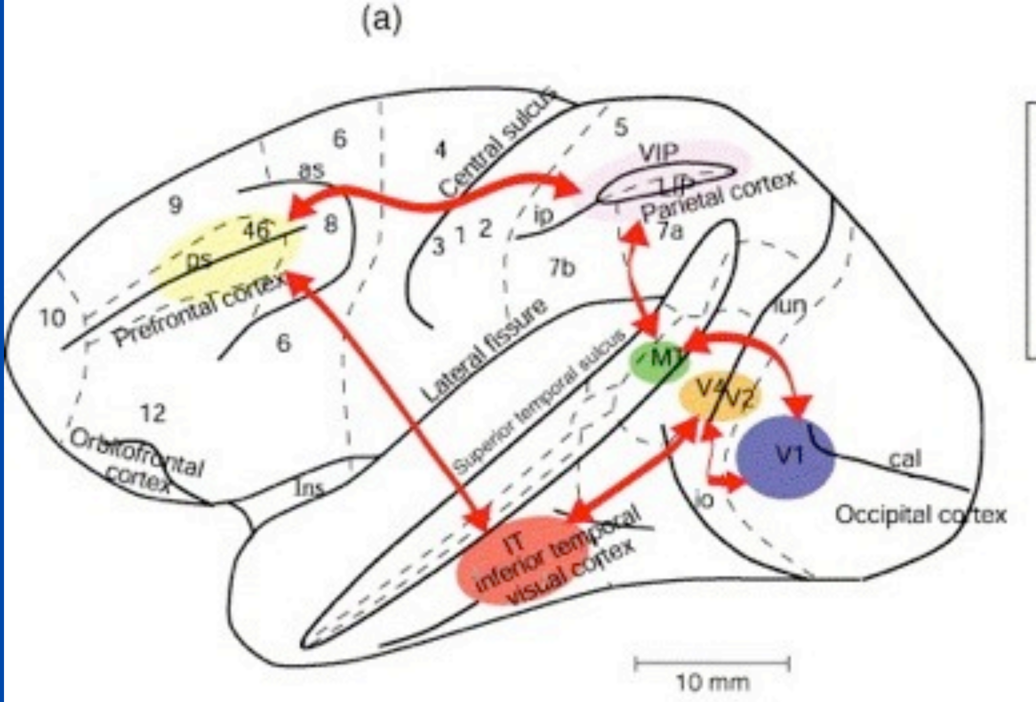
Intrinsic competitive mechanisms within specific cortical areas ,and forward and back projections between different cortical domains may also contribute to the preference for some courses of action over others

Cortical circuits have an attractor dynamics that limits the number of alternative courses of action that are available at a given moment



Emergent action selection

Selective attention, arising as the result of distributed competitive processes within and between brain regions may help to narrow the range of options available



Visual streams in macaque brain. Processing in each area, even the primary visual cortex, is subject to both top-down and bottom-up influences. From Deco & Rolls, 2005

Conclusions

- Nervous systems exploit a form of modularity (near decomposability) but modularity raises the problem of integration (action selection), the first brain may even have had action selection as its primary role
- Evidence suggests multiple substrates for action selection in the vertebrate nervous system
- A key proposal is that vertebrates exploit specialized selection circuitry found in groups of centralized brain structures—the basal ganglia and medial core of the reticular formation
- The connectional economy of this design may be one the reasons that the vertebrate nervous system has scaled successfully with the evolution of animals of larger brain and body size