Modelling Natural Intelligence

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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.

Active Vision Laboratory (leader: Kevin Gurney)

Active Touch Laboratory (leader: Tony Prescott)
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
Layered Control Architectures in Robots and Vertebrates

TONY J. PRESCOTT, PETER REDGRAVE, AND KEVIN GURNEY

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COMMENTARY

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

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

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

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

Mark D. Humphries, Tony J. Prescott

The basal ganglia in robotics: from robots to membranes

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

Tony J. Prescott and Carl Bilton
Department of Psychology
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

Metazoans

- Sponges (Porifera)
- Cnidarians (hydra, most jelly fish, anemones)
- Urbilaterians (Flatworms)
- Arthropods (Molluscs, Annelids, Nemerteans, Protostomes)
- Chordates (Hemicordates, Echinoderms, Deuterostomes)

- Multicellularity
- Radial Symmetry
- Bilateral Symmetry
- Hox gene expression

Adapted from Raff, 1996.
Great moments in evolution

Metazoans

Multicellularity

Radial Symmetry

Hox gene expression

Bilateral Symmetry

Urbilaterians

Flatworms

Protostomes

Deuterostomes

Arthropods
Molluscs
Annelids
Nemertean

Sponges (Porifera)

Cnidarians
(hydra, most jelly fish, anenomies)

Adapted from Raff, 1996.
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.
Aurelia aurita (scyphomedusa)

aka “Moon jelly”
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
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
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.
Aglantha Digitale (hydromedusae)
Aglantha swimming behaviour

Slow Swimming (feeding)

Fast Escape

From Meech, 1995
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

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)
Great moments in evolution II

Flatworms
Brains and bilaterality

- Sponges (Porifera)
- Cnidarians (hydra, most jelly fish, anenomes)
- Urbilaterians (Flatworms)
- Arthropods
  - Molluscs
  - Annelids
  - Nemerteans
  - Protostomes
- Chordates
  - Hemichordates
  - Echinoderms
  - Deuterostomes

- Bilateral Symmetry
- Hox gene expression
- Radial Symmetry
- Multicellularity

Metazoans

Adapted from Raff, 1996
Brains and bilaterality

Adapted from Raff, 1996
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)

Precambrian meander
(Crimes and Anderson, 1985)

‘Tight’ meander
(Seilacher, 67)
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.

From Gruber and Ewer, 1962
The role of the flatworm brain in behaviour (2)

Typical feeding behaviour of normal and decerebrate worms

Notoplana Acticola

From Koopowitz and Keenan, 1982
The role of the flatworm brain in behaviour (2)

Typical feeding behaviour of normal and decerebrate worms

*Notoplana Acticola*

From Koopowitz and Keenan, 1982
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

**Thigmotaxis**—stay close to tracks

**Phobotaxis**—avoid recrossing tracks

_Spirodesmos_ (Huckriede, 1952)
Decussating neurons in flatworm brains

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.

*Dye-stained neurons in Notoplana acticola, from Koopowitz, 1986*
Modelling a meandering trace-maker

Taphrelminthopsis
(Frey & Seilacher, 80)
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, anenomes)
- Flatworms (Platyhelminthes)
- Arthropods (Molluscs, Annelids, Nemerteans, Protostomes)
- Chordates (Inc. Vertebrates, Echinoderms, Deuterostomes)

Multicellularity

Metazoans

Radial Symmetry

Bilateral Symmetry

Hox gene expression

Adapted from Raff, 1996
Vertebrate nervous systems

Metazoans

Multicellularity

Radial Symmetry

Bilateral Symmetry

Hox gene expression

Chordates
Inc. Vertebrates
Echinoderms
*Deuterostomes*

Arthropods
Molluscs
Annelids
Nemerteans
Protostomes

Flatworms
(Platyhelminthes)

Cnidarians
(hydra, most jelly fish, anenomies)

Sponges
(Porifera)

Adapted from Raff, 1996
Deuterostomes (non vertebrate)

Echinoderms - Pentameral Symmetry

Hemichordate worm

Tunicates

Tunicate larva

Chordates

Amphioxus
First Vertebrates

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

From Shu et al., 1999

Sansom et al. 2010
First Vertebrates

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

From Shu et al., 1999

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

From Valentine, 1994

From Gabor Milkos & Campbell, 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)*
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)

Brain of a lamphrey
Modern vertebrate brains: diverse shapes and sizes, common structures

Adapted from Rosenzweig et al. 1999
Generic plan of the vertebrate brain

Based on Butler and Hodos, 1996
Generic plan of the vertebrate brain

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)
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.

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Adaptive Behavior 1999, 7(4), 99-127

Layered Control Architectures in Robots and Vertebrates

TONY J. PRESCOTT, PETER REDGRAVE, AND KEVIN GURNEY

University of Sheffield, UK
Layered architecture for vibrissal control

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

Adapted from Kleinfeld, Ahissar, and Diamond, 2006
Layered architecture for vibrissal control

From Diamond et al. 2008

Adapted from Kleinfeld, Ahissar, and Diamond, 2006

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Layered architecture for vibrissal control

From Diamond et al. 2008

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

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Computational models of the basal ganglia: from robots to membranes

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²Department of Anatomy and Structural Biology and The Neuroscience Centre, University Otago, Dunedin, New Zealand
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.
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
Embedded in robots

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

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The ventral basal ganglia, a selection mechanism at the crossroads of space, strategy, and reward.
The reticular formation
A brainstem substrate for behavioural integration?

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.