The evolution of action selection[1]

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1   Introduction

Action selection is the task for the 'whole iguana' of resolving conflicts between competing behavioral alternatives. This problem has received considerable attention in the growing adaptive behavior literature (see reviews in Maes, 1995; Prescott, Redgrave, and Gurney, 1999) much of which has built on earlier research in ethology (see. e.g. McFarland, 1971; McFarland, 1989) where it is also described as the task of 'decision making', 'behavior selection', or 'behavior switching'. Whichever label is used, it is useful to recognise at the outset that the problem of selecting actions is really part of a wider problem faced by any complete creature, that of *behavioural integration—*

"the phenomenon so very characteristic of living organisms, and so very difficult to analyse: the fact that they behave as wholes rather than as the sum of their constituent parts. Their behaviour shows integration, […] a process unifying the actions of an organism into patterns that involve the whole individual." (Barrington, 1967 p. 415)

In discussing control systems for mobile robots, Brooks (1994) has emphasised a similar notion of *behavioral coherence* which he places at the centre of the problem of autonomous agent design. As robots have become more complex, they have naturally gained an increasing variety of actuator sub-systems, many of which can act in parallel. Controlling robots therefore requires the co-ordination, in space and time, of many interacting sub-systems, and the allocation of appropriate resources between them. The problem for control system design is to satisfy these multiple constraints in a manner that maintains the global coherence of the robot's behavior. Given this context, Brooks raises the concern that research directed at the more specific problem of action selection may not lead to automatic progress in the design of systems with behavioral coherence. It may be the case, for instance, that proposed action selection mechanisms will not scale-up to the task of controlling more complex robots; or, that we may come to see effective action selection as a consequence of maintaining behavioral coherence, rather than as a key element involved in creating it.

What concerns us here, of course, is the question of the decomposition of control. Will an effective robot control architecture have components whose role is

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recognisably to resolve conflicts between different action sub-systems? Or, is action selection better regarded as an emergent property—the consequence of many and diverse interactions between multiple sub-systems? (and, in this sense, not something to be considered in isolation from other aspects of control). If effective integration is emergent then research on the design of action selection mechanisms *per se* may lead to a dead-end. On the other hand, if action selection or other related aspects of behavioural integration, can be implemented in specialised system components then some of the advantages of modularity may accrue to the whole design process. Specifically, it may be possible to add/delete/modify different action sub-systems with less concern for the possibility of adverse, system-wide consequences for the maintenance of behavioral coherence[2].

How are we to decide answers to these questions? Our strategy in this chapter is to attempt a brief survey of some relevant characteristics in the design of natural control systems for complete creatures—animal nervous systems. Our focus will be on those aspects of the functional architecture of nervous systems that seem to play an important role in action selection, or, more broadly, in behavioral integration. In particular, we will look for evidence of structures that are specialised to resolve conflicts and that seem to have this as their primary function. The absence of such structures would favour the view that action selection is most often the emergent consequence of the interaction of sub-system elements concerned with wider or different aspects of control. Such findings might encourage us to pursue similar, distributed solutions to the coordination of complex robot control systems. The presence of candidate structures, on the other hand, would favour the view that complex control architectures can have a natural decomposition into components concerned with the sensorimotor control of action, and those concerned with the selection of action. Such findings would suggest a similar strategy for the decomposition of robot control. To anticipate our argument somewhat, we will be making the case that nervous system evolution *does* show evidence of specialised action selection mechanisms in some complex natural control systems.

Our approach is also an evolutionary one in that we will specifically consider animal nervous systems at three different and important grades in the evolution of complex metazoans (multicellular animals). To place what follows in this evolutionary context, figure 1 shows a phylogeny of the major metazoan phyla illustrating some of the principle early events in the evolution of animal body plans and nervous systems.

From the perspective of this chapter, the first event of particular note is the evolution (node 2 in the figure) of neurons and *nerve nets* in animals of the phylum *cnidaria*.

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[2] A full discussion of the pros and cons of emergent and specialised action selection, particular with respect to the notion of modularity, is given in Prescott et al. (1999).

This phylum includes a host of relatively simple, but also very intriguing animals such as jellyfish, sea anemones, corals, and hydrozoa (e.g. *Hydra*). These differ from the most primitive metazoa (the sponges—*porifera*), in that they possess a variety of different tissue types; generally possess a radial symmetry; may have simple sensory organs; and have nervous systems composed of networks of nerve cells. Fossil evidence suggests that cnidaria were present in the Precambrian era (i.e. more than 550 mya[3]), and are therefore likely to have been the first animals to evolve nervous systems of any kind. There is still a great deal to be learned about the functional architecture of cnidarian nervous systems, however, existing research does provide a number of very interesting pointers. Some of this evidence is reviewed in section 2 below.
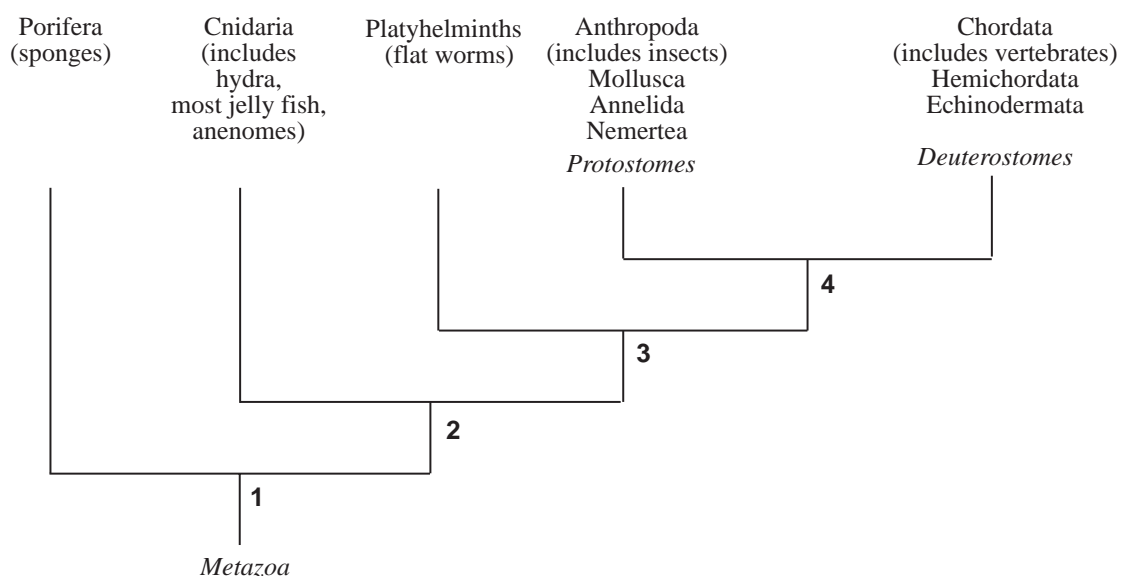

Figure 1. Phylogeny of early metazoans (based on Raff, 1996). Important evolutionary changes include 1. multicellularity, 2. Radial symmetry, different tissue types, nerve nets. 3. Bilateral symmetry, internal organs, central nervous systems, brains. 4. *Hox* gene expression in nervous system and body patterning.

The next event, node 3, separates the bilateral animals from the other metazoan phyla, and identifies the *platyhelminths* (the flatworms) as the most primitive form of bilaterian. Flatworms possess central nervous systems organised around a 'brain'. Animals of this sort are known to have been present in the Precambrian as demonstrated by the large number of *trace fossils* that have preserved the behavior (e.g. foraging trails) though not the body forms of worm-like animals from that period. Simulation of these trace fossil patterns indicates a capacity for intelligent coordinated behaviors not unlike that demonstrated in some simple behavior-based robots (Raup and Seilacher, 1969; Prescott and Ibbotson, 1997). Section 3 reviews a

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[3] Million years ago.

number of findings concerned the functional architecture of the nervous systems of living platyhelminths, and considers some of the insights that have been developed through trace fossil modelling into the nervous systems of early bilaterians.

Node 4 in our figure marks the beginning of a further momentous phase—the evolution of the metazoan phyla who share the use of the *Hox* regulatory gene cluster as a determinant of body patterning and nervous system organisation. Many diverse animal types are listed here that can be distinguished into two distinct groups, the *protostomes* and the *deuterostomes,* on the basis of early events in embryological development. It is interesting to note that the evolutionary line leading to the vertebrates (belonging to the phylum *chordata*), probably diverged at a very early stage from that leading to invertebrate groups with more 'advanced' nervous systems (insects, cephalopods, etc.)—the common ancestor of all these bilaterians being of only flatworm grade. Of the deuterostomes, in fact, vertebrates are the only animals with highly developed nervous systems, although the echinoderms—such as sea urchins, and starfish—with their pentameral (five-sided) symmetry certainly present some interesting problems (and solutions) in control system design!

Fossil evidence shows a remarkable explosion of animal forms during the Cambrian period (543–505 mya) in which all of the more advanced protostome and deuterostome phyla were represented, having been almost entirely absent from the fossil record at the end of the Precambrian. This evidence suggests the very rapid evolution of complex nervous systems as part of the general evolution of new body plans (Gabor Miklos, Campbell, and Kankel, 1994; Prescott and Ibbotson, 1997). Until recently there were no uncontroversial vertebrate fossils of earlier origin than the Ordovician period (~495 mya), implying that vertebrates appeared somewhat later than this general explosion of bilaterians. However, recent finds from Chengjiang in China (the Chinese 'Burgess shale') show the presence of fish-like creatures in the early Cambrian (Shu et al., 1999) —between twenty and fifty million years earlier than was previously thought. In Prescott et al. (1999) we have reviewed evidence supporting the conservation, through evolution, of a basic vertebrate brain plan which may have been present in early jawless fish (see also Gabor Miklos, 1994). Taken together, this evidence suggests that the first vertebrate nervous systems may be as ancient as any of those of the protostome bilaterian phyla. There is insufficient space to consider the many and varied forms of nervous system architecture seen in the protostome invertebrates. Instead, section 4 considers a number of aspects of the functional architecture of vertebrate brains that have implications for understanding how action selection occurs in vertebrates, while in section 5 we outline our proposal (Prescott et al., 1999; Redgrave, Prescott, and Gurney, 1999) that a group of structures in vertebrate brain known as the *basal ganglia* are critically involved in action selection and behavioral integration. This section also presents some initial results from our efforts to build an embodied (robotic) model of the vertebrate basal ganglia

that replicates interesting aspects of the behavior of our model animal, the laboratory rat.

Finally, in section 6, we summarise our review of the evolution of action selection mechanisms in animal nervous systems and look for implications that could inspire the design of control architectures for autonomous robots.

2   Cnidarian nervous systems

Whilst the most primitive metazoans, the sponges, lack neurons and respond only to direct stimulation (usually with a very slow, spreading contraction), cnidarians have quite complex nervous systems, composed, principally, of distributed *nerve nets,* and show both internally generated rhythmic behavior, and co-ordinated patterns of motor response to complex sensory stimuli.

The basic cnidarian nerve net is a two-dimensional network of neurons which has both a sensory and a motor capacity, and in which there is no distinction between axons and dendrites—nervous impulses therefore propagate in both directions between cells (Mackie, 1990). According to Horridge (1968), in the most primitive nerve nets "the spatial pattern is irrelevant, the connectivity pattern has no restrictions. […] any fibre is equivalent to any other in either growth or transmission" (p. 26).

The lack of intermediary forms of nervous system organisation between the aneural sponges and the cnidarian nerve net means that the evolutionary origin of nerve nets, and of nervous tissue in general, is shrouded in mystery. It seems likely, however, that neural conduction was preceded by more primitive forms of communication in which signals were propagated directly between neighbouring cells (indeed this form of non-neural communication exists alongside neural conduction in some cnidarians—Josephson, 1974). The evolution of the nerve net can then be understood as facilitating more rapid and more specific communication over longer distances, which would allow both quicker responses and increased functional diversification between different cell groups (Horridge, 1968; Mackie, 1990). Most of the neurophysiological features of more 'advanced' metazoan nervous systems are actually present at the cnidarian grade including multifunctional neurons, action potentials, synapses, and chemical neurotransmission. For Grimmelikhuijzen and Westfall (1995) the presence of such features shows cnidarians to be "near the main line" of evolution, and suggests that the study of their nervous systems will illuminate some of the properties of nervous systems ancestral to the higher metazoans.

The nervous systems of extant cnidarians are, in fact, more sophisticated than the above characterisation of simple nerve nets indicates. For instance, *Hydra*, one of the

more primitive living cnidarians, has a variety of different neuronal cell-types, and while most belong to diffuse networks, some are found in localised, well-defined bundles that may have specific functional roles (Josephson and Mackie, 1965; Mackie, 1990). In other cnidarians, such as the hydrozoan jellyfish, parts of the nerve net are fused to form longitudinal or circular tracts that allow very fast signal conduction and can support fast attack, escape, or defense reactions. Many of the free-living cnidarians also possess light-sensitive and gravity-sensitive organs that allow behaviors such as orientation, sun compass navigation, and daily migration (see, e.g. Hamner, 1995); unfortunately the neural substrate that supports such behaviors remains poorly understood.

What is known about the functional architecture of cnidarian nervous systems? Horridge (1956; 1968) describes the decomposition of the nervous system of the jellyfish *Aurelia aurita* into two distinct components: a network of bipolar neurons that controls the symmetrical, pulsed contraction of the bell and enables the animal to swim; and a second more diffuse network, consisting largely of small multipolar neurons, that is spread across the body, tentacles, and margins of the animal, and coordinates localized feeding movements. These two systems, which are illustrated in figure two for the larva of *Aurelia aurita*, have relatively few interconnections and show clear evidence of independent operation. A similar functional subdivision of the nerve net into two or more parts has also been noted in a variety of other cnidarians such as sea anemones. This behavioral decomposition of control, with physically distinct circuits for feeding and movement, clearly shows an interesting similarity to that proposed for behavior-based robots (see, e.g. Brooks, 1991; Mataric, 1997).

The question arises, however, are alternative decompositions of the nervous system possible? Meech (1995) describes a jellyfish, *Aglantha digitale,* in which a single nerve net can carry two different types of action potentials enabling either rapid escape swimming, or, slow rhythmic swimming for feeding. Similarly, the sea anemone *Actinia*, uses impulse patterns of different frequency to obtain distinct feeding and escape behaviors from a single nerve net (Mackie, 1990). Thus, there seems to be no strong requirement for a separate neural substrate for different classes of behavior in these animals.
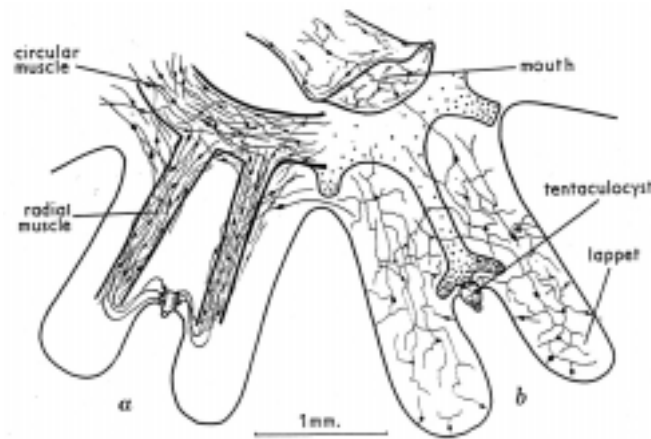
Figure 2. Nervous system of the ephyra larva of *Aurelia aurita,* showing, in two arms of the bell, a) the swimming network controlling the circular, and radial muscles; b) the diffuse nerve-net underlying feeding behaviour. A marginal ganglion is located at the base of each tentaculocyst. From Horridge (1956).

The lack of centralised nervous system components in cnidarians also leads to some interesting and elegant solutions to the problem of generating an integrated global response. For instance, consider the fast escape behavior of a jellyfish which can be triggered by contact at any point on the periphery of the animal. Since jellyfish swim by the synchronous, simultaneous contraction of the entire perimeter of the bell, the lack of centralised signalling presents an interesting control problem for which Mackie (1990) describes two contrasting solutions. One solution, seen in *Aglantha*, uses a giant axon with very fast conductance so that a single spike can circumnavigate the periphery in just a few milliseconds. An alternative and more remarkable solution, seen the much larger species *Polyorchis*, involves a ring of neurons that carries action potentials that change shape as they circle the bell. Successive muscles groups respond to these changing shapes by contracting at shorter and shorter latencies, thus ensuring a uniform and synchronised contraction of the whole perimeter. This elegant solution appears to depend solely on membrane-level properties of the neurons involved (Spencer et al., 1989).

According to Horridge (1956) the two functionally distinct nerve nets of *Aurelia aurita* make contact with one another in neuron clusters termed the *marginal ganglia*. Each ganglion is part of the swimming network and is involved in the regular beat of the swimming contraction; it can also generate its own regular pulse if isolated from other parts of the network (thus showing an intrinsic rhythm generating capacity). Each ganglion is also in contact with the diffuse network that underlies the feeding response. Excitation in the diffuse network can inhibit the swimming rhythm or, in some cases, accelerate the rhythm. This evidence suggests the possibility of a hierarchical arrangement: Pattern formation (the swimming beat) seems to be under the distributed control of multiple pace-maker systems, whilst the behavior of this

swimming network is under the modulatory control of the diffuse feeding network. If this is the case, then we could view this jellyfish nervous system as providing a natural example of a *subsumption architecture* (Brooks, 1986) composed of two distributed layers of control.

Cnidarian nervous systems demonstrate the ability of relatively simple nerve networks to support multiple behavioral modes, in some cases, using the same neural structures to generate two quite different patterns of activity. Whilst a likely physical substrate (the marginal ganglia) has been identified for the interaction between feeding and swimming in some jellyfish species there is no suggestion that these structures or pathways are exclusively involved in action selection. Although behavioral decomposition of function seems to be a probable cnidarian trait, decomposition involving specialised selection structures seems far less likely. On the contrary, cnidarian nervous systems seem rather good preparations in which to study behavioral integration as a global, emergent property of the control system architecture.

3   Flatworm nervous systems

The phylum *platyhelminthes* comprises the free-living *turbellarians* and the parasitic flukes and tapeworms. The focus here will be on the turbellarians as the consensus in modern zoology is that these animals provide a better indication of the ancestral characteristics of the phylum. In the evolution of bilateral animals a critical development was the appearance of a central nervous system organised around a massed concentration of nerve cells called the *cephalic ganglion*—the archaic brain. In flatworms we find the simplest living animals that possess this form of nervous system architecture (Reuter, 1989; Reuter and Gustafsson, 1995).

Flatworms are bilaterally symmetric having distinct anterior and posterior ends, and dorsal (upper) and ventral (lower) surfaces. Sensory systems are distributed symmetrically between the left and right sides of the body, but together with the nervous system often show a concentration, termed *cephalization,* towards the anterior end of the body. The free-living turbellarians range in size from a few millimetres to tens of centimetres. They are found in aquatic environments or moist terrestrial environments where most pursue a predatory or scavenging life-style requiring a repertoire of reasonably complex behaviors. Turbellarian nervous systems appear in a bewildering variety of different configurations, none of which can necessarily be considered primitive (Reuter, 1989). Typically, there are three to five pairs of major nerve cords connecting with the cephalic ganglion. These cords are interlinked by circular commissures (bands of nerve fibres), which themselves make connections with networks (plexuses) of nerves underlying muscular and/or epithelial tissue. The cell bodies of sensory neurons are found near the periphery while those of

motor neurons and interneurons are distributed throughout the nerve cords and the brain. The concentration of nerve cells into cords, fibres, and ganglia distinguishes this type of *central* nervous system from the nerve nets of the cnidaria.

Our discussion of the functional architecture of the flatworm nervous system follows the research of Gruber and Ewer (1962) and of Koopowitz and co-workers (Koopowitz, 1970; Koopowitz, Silver and Rose, 1975; Koopowitz, Silver and Rose, 1976; Koopowitz and Keenan, 1982; Koopowitz, 1989) which has focused on the role of the brain in marine polyclad turbellaria. Gruber and Ewer studied the effect of brain removal on the behavior of the polyclad *Planocera gilchristi*, whose nervous system is pictured in figure 3.
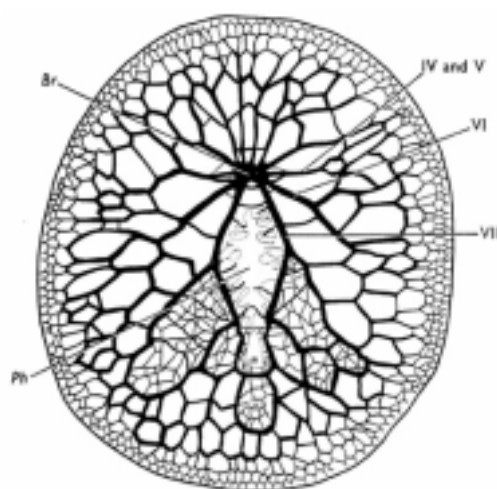

Figure 3. Nervous system of the turbellarian *Planocera gilchristi*, showing the brain (Br), pharynx (Ph), and major nerve cords (1V-VII). The finest granularity of nerve fibres is only shown in the central areas around the pharynx. From Gruber and Ewer (1962).

Planocera usually moves by swimming or crawling along the substrate. Swimming involves the generation of a transverse wave that moves backwards along the length of the body, while crawling involves a regular alternating extension of the two sides of the body. Following brain removal, Gruber and Ewer reported that components of both normal swimming and normal crawling were present in decerebrate animals but that these were never integrated into the normal sequences—the overall movement of the animal was irregular and uncoordinated. Similarly, decerebrate animals lacked a normal rapid righting response when placed in an inverted position, although they could eventually right themselves by making writhing and twisting movements. These animals also failed to display the normal retraction response to mechanical stimulation, again responding with an uncoordinated writhing.

Gruber and Ewer also describe the effects of decerebration on the feeding behavior of *Planocera.* This behavior was the subject of further detailed investigation by

Koopowitz (1970) who went on to examine decerebrate feeding in another marine polyclad— *Notoplana* (Koopowitz et al.1975, 1976). The behavior of *Notoplana* will be described here as it is typical of the general pattern of results obtained with these animals.

In the intact polyclad worm presentation of a food item near to its posterior margin will cause it to extend a nearby portion of that margin and use this to take hold of the food. The animal will then rotate the anterior part of its body on that side, until the anterior margin comes into contact with the food. The posterior margin subsequently loosens its grip allowing the anterior edge to manipulate the food into the mouth. This sequence of behaviour is shown in figure 4a. When fed with large food items (dead shrimps) the animal becomes satiated after a few food presentations and the feeding response ceases.

In the decerebrate animal, in contrast, the body turn to bring the anterior margin into contact with the food is never observed. Instead, the animal performs a 'local feeding response' in which it gradually moves the food directly to its mouth via the underside of its body (figure 4b). In addition to the lack of a coordinated 'whole body' feeding response the decerebrate animals show no satiety and will continue passing food items towards the mouth even once the gut is completely full. Control experiments in which the brain remains intact but the main posterior nerves on one side of the body are severed, show feeding behavior characteristic of the normal animal on the intact side, and that characteristic of the decerebrate on the cut side.
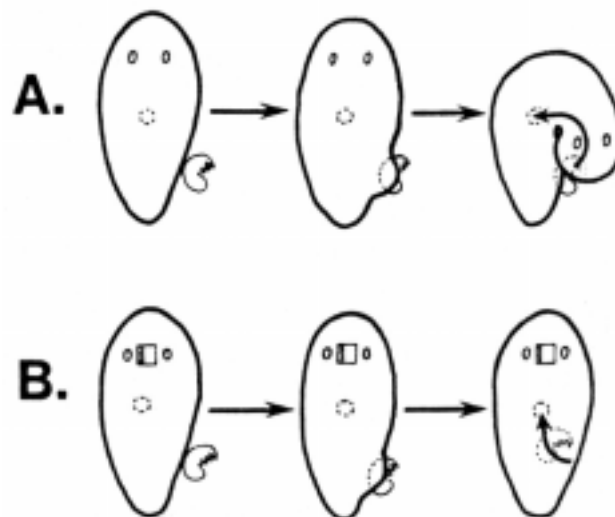

Figure 4. Feeding behavior of the polyclad *Notoplana*. A. In the intact animal contact with an item food at the posterior margin causes a whole body response in which the animal turns and grabs the food with its anterior edge before passing it to the central, ventrally located mouth. B. In the decerebrate animal, a 'local feeding response' causes food to be passed directly to the mouth. From Koopowitz and Keenan, 1982.

Overall, these experiments on decerebrate polyclad behavior demonstrate the role of the brain in regulating local reflexive actions whose neural substrate is located in the periphery of the animal. In the case of crawling and swimming, the brain orders the temporal sequence of local activity in different marginal areas of body. In the case of feeding, the brain holds the 'local feeding response' under inhibitory control whilst enabling actions involved in the 'whole body' feeding response.

The centralized coordination of integrated behavior seen in the polyclad stands in interesting contrast to the distributed nature of control noted in the cnidaria. What evolutionary pressures may have brought about such a significant change in the functional organization of nervous systems? Koopowitz and Keenan (1982) contrast two possible explanations for the evolution of the first brains. The first possibility is that the brain is one of several consequences of the process of cephalization—the aggregation of sensory systems in the anterior portion of the animal. According to this explanation, the co-ordination of peripheral mechanisms becomes focused in the brain in order to place it closer to the principle sources afferent stimulation. This view also makes the primary role of the archaic brain one of response initiation. The alternative view, favoured by Koopowitz and Keenan, is based on the observation that although *all* polyclads have brains, only a few have a significant degree of cephalization. Instead, the origin of the brain is attributed to a more fundamental change in the body plan of the organism—the evolution of *bilateral symmetry:*

"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)

From the perspective of this chapter, this interesting proposal might be paraphrased as the hypothesis that the brain first evolved as a centralised mechanism for action selection. Koopowitz and co-workers (1970, 1982, 1989) also describe further experiments in which half of the polyclad brain is excised, and the severed cephalic nerve cords allowed to regrow, re-establishing appropriate functional connections with the remaining half of the brain. In other experiments the brain of one animal is transferred in its entirety into another's body and once again re-exerts many of its original behavioral controls over peripheral systems. Finally, brain-control returns even if the brain is re-inserted upside-down or rotated 180° (try doing this with a robot's CPU!). This robustness of function is particularly remarkable given that the brain is clearly much more than a relay station between the two halves the animal, but

instead plays an integrative role in selecting appropriate patterns of peripheral motor acts.

Robot modelling of the behavior of early bilaterians

The turbellarian nervous systems we have been considering are particular interesting because of the position occupied by the phylum platyhelminthes in the evolutionary history of animal life. The common ancestor of all modern, bilaterally symmetric, animals was probably a creature of little more than flatworm grade that lived in a shallow marine environment during the Vendian period (544 to 565 million years ago) of the late Precambrian [43]. Such animals, and many of the organisms (worms, mollusks, and arthropods) they gave rise to, left no actual fossils as they had virtually no hard body-parts. Fortunately, however, they did leave a fossil record of sorts—the tracks, trails, and burrows of some early invertebrates have been preserved forming what are now called trace fossils. The earliest foraging trails, which are sometimes called 'scribbles', show tracks that often cross themselves, and indicate relatively crude foraging strategies. By the end of the Vendian, however, more regular foraging patterns were appearing that formed spiral fossils or 'meandering' trails that loop back on themselves without crossing. One such fossilized meander, dating from the late Precambrian, is shown in figure 5.
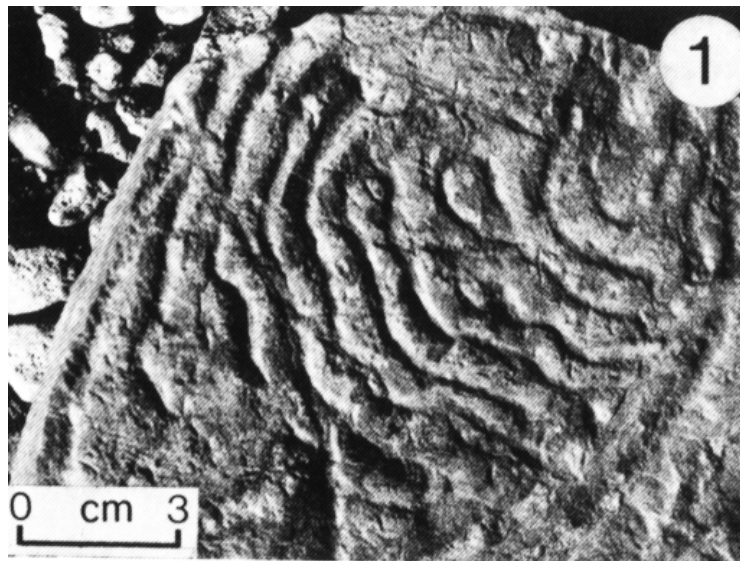

Figure 5. A Precambrian meandering trace fossil. (Crimes and Anderson, 1985).

In attempting to infer the behavioral capabilities of the ancient animals that left fossil traces, it seems reasonable to seek the simplest mechanisms that will reproduce the observed patterns. In 1969, the geologists Raup and Seilacher published an article demonstrating that computer simulations of meandering trace fossil patterns could be created by combining a number of simple reactive behaviors: *thigmotaxis*, stay close to previously formed tracks; *phobotaxis*, avoid crossing existing tracks; *strophotaxis* make 180° turns at various intervals; and move forward (*advance)* when the

conditions of the other behaviors are not met. The principle of a complex behavior pattern emerging from the interaction of a number of simple reactions is a characteristic that this early work in computer modelling clearly shares with the 'behavior-based' approach in robotics. Indeed, Raup and Seilacher's meander generator bears striking similarities to many of the 'wall-following' mechanisms that have been used in the control of behavior-based robots. For instance, Mataric (1990) describes a robust wall-following behavior that emerges from the interaction of three modules. The first, similar to thigmotaxis, causes the robot to steer inwards (toward the wall) when sensors indicate that the distance to the wall is above some threshold; the second, similar to phobotaxis, causes the robot to steer outwards when the sensed distance is below a threshold; while, the third, causes the robot to move forward whenever the conditions of the other two behaviors are not met.

This fascinating intersection between evolutionary biology and robotics inspired us to make our own investigations into robot trace-making behavior using a custom-built robot that could generate and follow trails across the laboratory floor (Prescott and Ibbotson, 1997). The sediment feeders of the Precambrian probably used chemical and mechanical sensory systems to detect and follow their tracks and burrows, however, as a (very) loose approximation to these mechanisms our robot used light sensors to detect a trail of paper which was dispensed by the robot as it moved across the laboratory floor. Figure 6 shows how the different component reactions that are required for (paper)-trail making can be easily implemented by a robot.
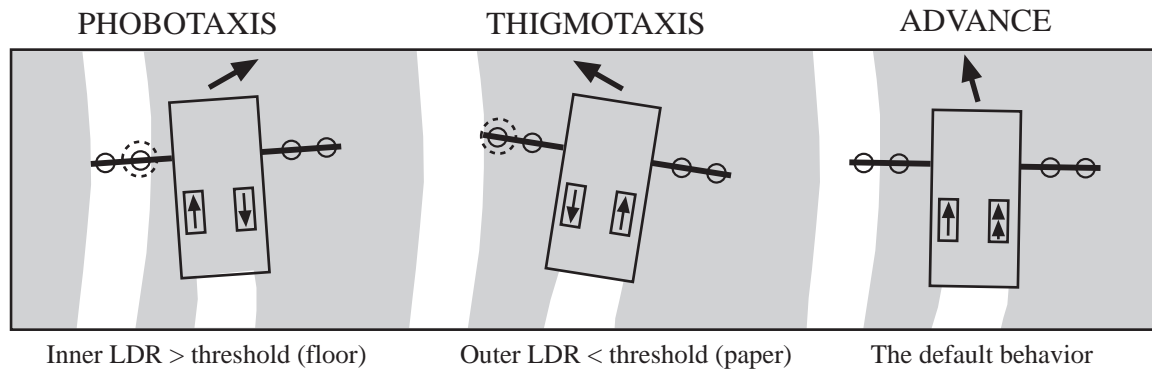

PHOBOTAXIS	THIGMOTAXIS	ADVANCE
Inner LDR > threshold (floor)	Outer LDR < threshold (paper)	The default behavior

Figure 6. Implementing trail making behavior in a robot. The robot has two arms (right and left) each carrying two light sensors (LDRs) and two motors (right and left). *Phobotaxis* (left), a turn away from the sensor arm, is triggered when the value of the inner LDR sensor is greater than a threshold set slightly above the reflectance of the dark floor surface. *Thigmotaxis* (center), a turn towards the sensor arm, is triggered when the value of the outer LDR sensor is less than a threshold set slightly below the reflectance of the light-coloured paper dispensed by the robot. In both cases the required turn is achieved by rotating the drive wheel on the outside of the turn forwards and that on the inside of the turn, in reverse. For the *advance* behavior (right) the robot moves forward on a trajectory that drifts inwards towards the sensor arm. To allow trail making phobotaxis should suppress thigmotaxis which should suppress the advance reaction (from Prescott & Ibbotson, 1997).

The three behaviors illustrated in figure 6—phobotaxis, thigmotaxis, and advance—are sufficient to generate a *spiralling* trail as long as the robot is controlled by just one of its two sensor arms (the robot will then spiral in the direction of the active sensor arm). However, if both sensor arms are active then the two sides will send conflicting signals to the motors causing the robot to move off-course. In order to generate a *meandering* trail. (i.e. one containing U-turns) an additional strophotaxis mechanism is needed that will swap control of the robot from one sensor arm to the other. Figure 7 shows the meandering trail generated by a robot that uses ''time outs' to control strophotaxis, in other words, control is swapped between the two sides of the robot at fixed time intervals. Note that as soon as control is swapped from one side to the other, the self-correcting nature of the thigmotaxis/phobotaxis reactions will cause the robot to turn until contact is regained with the trail on the opposite side (so the U-turn itself is not explicitly programmed).

Figure 7. A robot meander. Control is passed from one side of the robot to the other every thirty seconds. Note the 'starter spiral' which is the result of 'trail following' where there is no initial trail to follow. Similar starter spirals are also seen in many meandering trace fossils. (from Prescott & Ibbotson, 1997).

It is interesting to consider this 'meander' control system in the context of the research we reviewed above on the role of the flatworm brain. The core components of the meander generator, the thigmotaxis and phobotaxis reactions, are reflexive mechanisms associated with peripheral sensors. However, a further crucial part of the control system is the component that suppresses signals from one side of the body while the other side is active, or which switches control of the motor system from one set of peripheral mechanisms to another. For Koopowitz and Keenan the flatworm

brain is primarily a mechanism that prevents the two sides of the body "from engaging in contradictory activities". We might speculate that this will also have been true of the nervous systems of the early, meandering fossil makers. In other words, that the appearance of efficient foraging trails in the fossil records of the Precambrian may mark the point where centralized action selection mechanisms had evolved to take control over peripheral reflex systems.

4   Vertebrate nervous systems

The evolution of the vertebrate nervous system is a critical unsolved problem in evolutionary neurobiology. Vertebrates belong to the phylum *chordata* whose members all possess, at some stage in their development, a single, hollow nerve cord, called the neural tube*,* which runs most of the length of the longitudinal body axis. Unfortunately, all living protochordates[4] have relatively simple nervous systems, and only one species, *Branchiostoma* (previously known as *Amphioxus*), has a nervous system that could resemble a transitional stage between ancestral chordate and vertebrate. *Branchiostoma* shows elaborations at the anterior end of the neural tube that may be homologous to some regions of the vertebrate brain (Lacalli, 1996); however the 'brain' of *Branchiostoma* is tiny, it sensory systems are primitive, and its behavior is very simplified compared with that of living vertebrates. In the modern fauna, the most primitive vertebrate characteristics are found amongst the jawless fish (*Agnatha).* Examination of these animals has shown the same gross morphological divisions of the nervous system—spinal cord, hindbrain, midbrain, and forebrain—as are present in other vertebrate classes. Indeed, impressions of these structures have also been found in the fossilized endocasts (casts from the inside of fossil skulls) of ancient agnathans. This evidence suggests that a basic 'ground plan' for the nervous system is shared by all living vertebrate classes, and possibly by all ancestral vertebrates (see Prescott et al, 1999).

The substrate for action selection in a control architecture as complex as the vertebrate nervous system is likely to involve many different mechanisms and structures. In the following we review a number possible candidates.

Conflict resolution at the final point of entry to the motor resource
One of the requirements for effective action selection is timely, sometimes very rapid, decision making. Transmission and response times in neural tissue are not negligible so for urgent tasks it is important to ensure that time is not lost resolving conflicts with competing behaviors. Recent evidence suggests, that for tasks such as defensive

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[4] The protochordates are all the animals of the chordate phylum excluding the vertebrates.

escape, special circuitry may have evolved in the vertebrate nervous system to provide a very fast override of the competition. The giant Mauthner cells found in the brain-stem of most fish and some amphibians provide an example of this function. Mauthner cells are known to be involved in the 'C-start' escape maneuver—the primary behavior used by many species of fish to avoid hazards such as predation. Eaton, Hofve, and Fetcho (1995) have argued that the principle role of the Mauthner cell in the brainstem escape circuit may not be to initiate the C-start but to *suppress competing behaviors*. This conclusion is supported by evidence that removal of the Mauthner neurons does not disable the C-start or have a marked effect on the strength or latency of the response. Instead, the fast conduction of the Mauthner giant axon (one of the largest in the vertebrates) may be crucial in ensuring that contradictory signals, that could otherwise result in fatal errors, do not influence the motor output mechanisms. Conservation of brain-stem organization across the vertebrate classes suggests that homologous mechanisms may play a similar role in the escape behaviors of other vertebrates[5].

Fixed priority mechanisms

Many studies of the role of the vertebrate brain in behavioral integration suggest that the resolution of conflict problems between the different levels of the neuraxis (spinal cord, hind-brain, mid-brain, etc.) may be determined by fixed-priority, vertical links. For instance, in (Prescott et al., 1999) we have reviewed evidence that 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 (using mechanisms somewhat similar to the inhibition and suppression operators employed in the *subsumption architecture*). Fixed-priority mechanisms cannot, however, capture the versatility of behavior switching observed between the different behavior systems (defense, feeding, reproduction, etc.) found in adult vertebrates. Since dominance relationships between behavior systems can fluctuate dramatically with changing circumstances more flexible forms of selection are required than can be determined by hard-wiring.

Recurrent reciprocal inhibition

A specific form of neural connectivity, which is often associated with action selection, is mutual or reciprocal inhibition. In networks with *recurrent reciprocal inhibition* (see e.g. Gallistel, 1980) two or more sub-systems are connected such that each one has an inhibitory link to every other (see figure 8, left). Such circuits make effective action selection mechanisms since the most strongly activated sub-system will receive less total inhibition than any of the others; the recurrent connectivity of the system rapidly maximises the activity of this 'winner' relative to all the other 'losing' sub-

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[5] Of course, the involvement of giant fibre systems in escape is common to many metazoan animals although it remains to be seen whether the decomposition proposed by Eaton et al. (1995) between initiating escape and suppressing competing responses will be found in other classes.

systems. Reciprocal inhibitory connectivity has been identified in many different areas of the vertebrate brain (Windhorst, 1996) although its functional role in most situations is not clearly understood. Gallistel (1980) has suggested that such circuits could play a role in conflict resolution at multiple levels of the vertebrate nervous system.
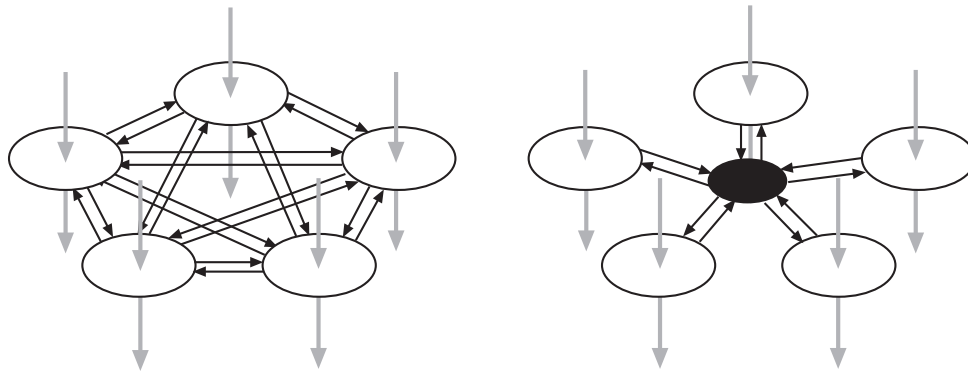

Figure 8. Distributed recurrent reciprocal inhibition network (left), compared with a 'central switch' selection mechanism. The latter has a significant advantage in terms of economy of connection costs. Dark arrows indicate one-way inhibitory connections, light arrows indicate sensory inputs and motor outputs.

Centralised selection mechanisms
Snaith and Holland (1990), following McFarland (1965), have contrasted a distributed action selection based on recurrent reciprocal inhibition with a system that employs a specialized, central switching device (see figure 8, right). They note that to arbitrate between *n* competitors, a distributed system with full connectivity requires *n(n-1)* inhibitory connections, while adding a new competitor requires a further *2n* connections. In contrast, a system using a central switch requires only two connections per competitor (to and from the switching mechanism) resulting in *2n* connections in all. Adding a further unit requires only *two* additional connections. Clearly, on this comparison, a central switching device provides a significant advantage in terms of economy of connections costs.

Ringo (1991) has pointed out that geometrical factors place important limits on the degree of network interconnectivity within the brain. In particular, larger brains cannot support the same degree of connectivity as smaller ones—significant increases in brain size (as have been seen in vertebrate evolution) must inevitably be accompanied by decreased connectivity between non-neighboring brain areas. Since functional units in different parts of the brain will often be in competition for the same motor resources, the requirement of lower connectivity with increased brain-size therefore strongly favors selection architectures with lower connectional costs.

We have recently proposed (Redgrave et al.1998; Prescott et al., 1999) that a group of functionally related structures in the vertebrate brain, called the *basal ganglia,* appear to be suitably connected and configured to serve the function of an array of specialized central switching devices that could provide effective conflict resolution with economical interconnectivity. In the following section we briefly review some of the evidence in support of this proposal and outline a robot model we are currently developing to demonstrate that the basal ganglia can function in the proposed manner.

5　　The vertebrate basal ganglia viewed as an action selection device

The principle components of the basal ganglia include the *striatum* and *pallidum* in the base of the vertebrate forebrain, and the *substantia nigra* and *ventral tegmental area* in the midbrain.　These structures (or homologous nuclei) are found in the nervous systems of all classes of jawed vertebrates and possibly in all vertebrates (Medina and Reiner, 1995 Northcutt, 1994). 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). Figure 9 shows the main basal ganglia nuclei and some of their intrinsic and extrinsic connections within the mammalian brain.
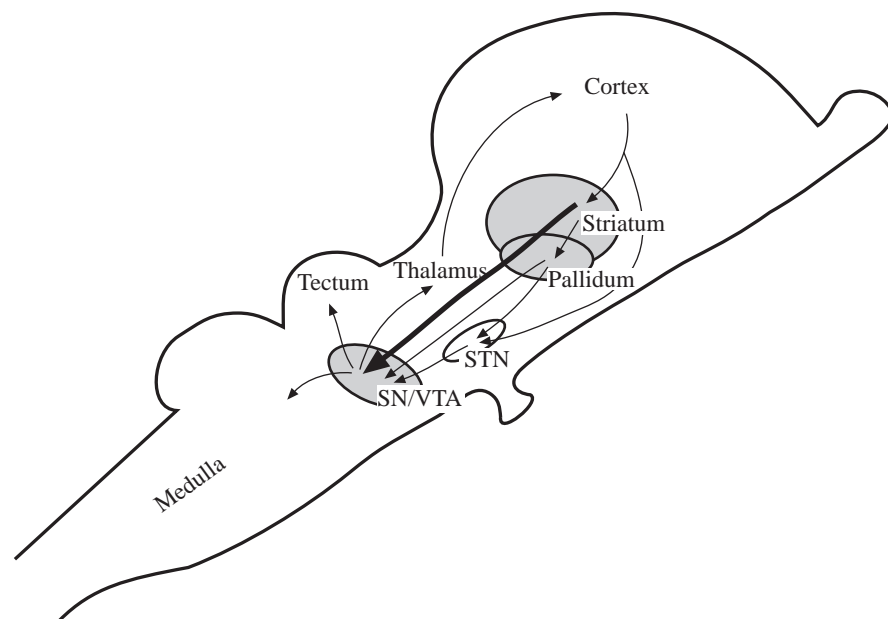

Figure 9. Diagrammatic representation of the principle structures of the vertebrate *basal ganglia* showing some of their intrinsic and extrinsic connections in the mammalian brain. Abbreviations: SN/VTA—substantia nigra/ventral tegmental areas, STN—subthalamic nucleus. From Prescott et al. (1999).

The proposal that the basal ganglia are involved in action selection is based on a growing consensus amongst neuroscientists that a key function of these structures is to enable desired actions and to inhibit undesired, potentially competing, actions (e.g.

Chevalier and Deniau, 1990; Salamone, 1991; Groenewegen, Wright and Beijer, 1996; Mink, 1996). The following provides a brief summary of the proposed functional architecture, a full account of this view has been provided elsewhere (Redgrave et al. 1998; Prescott et al. 1999).

The main *output* centers of the basal ganglia (parts of the *substantia nigra*, *ventral tegmental area*, and *pallidum*) are tonically active and direct a continuous flow of inhibition at neural centers throughout the brain that either directly or indirectly generate movement. This tonic inhibition places a powerful brake on these movement systems such that the basal ganglia seem to hold a 'veto' over all voluntary movement.

Neural signals which may represent 'requests for access' to the motor system are continuously projected to the *striatum* (the principle basal ganglia input nucleus) from relevant functional sub-systems in both the brainstem and forebrain of the animal. Afferents from a wide range of sensory and motivational systems also arrive at striatal input neurons. This connectivity could allow both extrinsic and intrinsic motivating factors to influencing the strength of rival bids. The level of activity in different populations of striatal neurons (*channels*) may then form a "common currency" in which competing requests for actuating systems can be effectively compared.

Intrinsic basal ganglia circuitry appears to be suitably configured to resolve the selection competition between multiple active channels and selectively *disinhibit* winning action sub-systems. The various basal ganglia nuclei have a rich interconnectivity, partly illustrated in Figure 9, whose function is only partly understood. Mink (1996) has reviewed anatomical and electrophysiological evidence from the mammalian basal ganglia indicating that the different intrinsic pathways provide complementary mechanisms that act to focus activity in the basal ganglia output nuclei—disinhibiting a desired channel while maintaining or increasing inhibition on competing channels. This proposal has been explored and extended in our own recent computational model of basal ganglia intrinsic circuitry (Gurney, Prescott and Redgrave, 1998; Gurney, Redgrave and Prescott, 1999).

It is interesting to note that reciprocal inhibition within the striatum probably provides one of the mechanisms that helps to resolve selection competitions (Wickens, 1997). The axon collaterals of individual striatal neurons typically occupy an area of about 0.5 mm in diameter, so recurrent inhibition can be expected to occur in local regions of approximately this size. By implementing this form of distributed switching within limited areas of the striatum the vertebrate brain may have evolved to exploit the potential of recurrent reciprocal inhibition whilst minimizing the cost of inter-competitor connectivity— employing a micro-scale distributed switch within a centralized selection mechanism.

Lesions, and neurochemical or electrophysiological interventions in basal ganglia structures have been shown to effect various aspects of behavior selection and

switching in a number of different experimental paradigms. Depending on the site and nature of the intervention, these effects include changes in the dominance relations between behaviors, reductions or increases in switching relative to controls, changes in variability of behavior, and failure to complete behaviors. The basal ganglia therefore appear to be heavily implicated in maintaining appropriate frequency and timing of behavior switches in the normal state. The symptoms of various brain disorders associated with the basal ganglia also suggest a role in action selection. Human disorders in which theses structures are implicated include: Parkinson's disease, whose symptoms include slowness and difficulty in making voluntary movements; Huntington's disease and Tourette's syndrome, characterized by excessive or inappropriate movement; and obsessive-compulsive disorders marked by repetition of certain stereotyped activities. Recent evidence suggests that these disorders may be related to abnormal levels of the neuromodulator *dopamine* in the basal ganglia. An important role of dopamine appears to be to moderate the balance between the different control pathways through the basal ganglia. A deficit of dopamine, such as is seen in Parkinson's leads to too much inhibition on motor systems. Excess dopamine, on the other hand leads to the excessive movement seen in Huntington's disease and Tourette's syndrome, or causes certain activities to become over-dominant as seen in obsessive-compulsive disorders.

Behavioral integration and the basal ganglia.
Further insight into the role of the basal ganglia within the overall control architecture of the vertebrate brain can be gained by considering circumstances in which basal ganglia circuitry is either disconnected or made inoperative. For instance, a number of studies have looked at the effect of blocking the outputs from the basal ganglia to midbrain movement generators such as the rat superior colliculus (see Dean, Redgrave, and Westby, 1989). From our perspective this can be viewed as jamming the switching circuit into the 'on' position (no basal ganglia inhibition of the motor system). In these circumstances the animal has no difficulty in co-ordinating the head and mouth movements required to locate and bite an object moving in its whisker field. At the same time, however, the animal appears unable to resist orienting to any tactile stimulus placed in the whisker field and fails to habituate to such a stimulus (Dean et al., 1989; Redgrave, personal observation). This inability to suppress an activated, but non-salient, action sub-system indicates a dissociation between the circuitry which controls switching (in the basal ganglia), and that which controls planning and execution of the motor act (in the colliculus and elsewhere in the brainstem).

Other research has looked at the effect of jamming the basal ganglia in the 'off' position. For instance, Teitelbaum and co-workers have performed extensive observational studies using animals with lesions of the lateral hypothalmus (reviewed in Teitelbaum, Schallert and Whishaw, 1983; Teitelbaum, Pellis, and Pellis, 1990).

Such lesions destroy the dopaminergic inputs to the striatum and result in continuous inhibition of all motor systems. Experimental animals show no spontaneous, environmentally-oriented movement for a day or so after the lesion operation and must be tube-fed to stay alive. With time, however, the ability to perform co-ordinated movements recovers to the extent that the animal will walk around, explore, and eat any palatable food it encounters. Behavior-generating mechanisms in the brain thus appear to be able to adapt so as to counteract the tonic inhibition from the basal ganglia. What fails to recover, in these circumstances, is the natural ease with which intact animals organize their actions into coherent motivated sequences. For example, recovered animals, whose behavior appears relatively normal, will often walk into a corner and stand for a long time making stereotyped stepping and head-scanning movements. Teitelbaum et. al. term this situation a "behavioral trap" and describe the animal's behavior as "disintegrated" and "disconnected from its usual adaptive outcome" (Teitelbaum et al., 1990 p. 101).

An embodied model of action selection in the vertebrate basal ganglia
A number of computational models of basal ganglia function have been investigated (Houk, Davis, and Beiser, 1995) both at the cellular and circuit levels of detail, but there are as yet few models that capture the distinctive neurodynamics of basal ganglia circuits while mimicking their behavioral functions. Our current research is directed at developing models of exactly this sort, and, as a first step, we have constructed a system-level simulation of the mechanisms operating within the basal ganglia selection circuit (Gurney et al., 1998, 1999). This model is based on the mammalian basal ganglia and is intended primarily as model of its function in the rat. As previously noted, activity in the basal ganglia can be modified in the biological setting by the effects of the neuromodulator dopamine. This has been incorporated into the model and we have shown that increased dopamine has the effect of making the current action selection more vulnerable to alternative competitors; in effect dopamine is capable of dynamically modulating the sensitivity of the selection mechanism (see also Redgrave, Prescott and Gurney, 1999).

An important goal has been to construct an embedded basal ganglia model in which selection occurs between multiple, physically-realised behaviors in a small mobile robot. Our specific program of research has been inspired by observing the behavior-switching of an adult rat in the square arena illustrated in figure 10. Here, bedding material from the animal's home cage is positioned in one shaded corner of the arena, and items of food are placed in a small dish in the center of the arena. When the rat is initially placed in this environment it shows exploratory behavior and thigmotaxis (staying close to the walls) and a strong preference for the 'nest' corner of the box. A common behavior on locating the food dish is to carry a food item back to the nest where it is consumed. The balance between locomotion, feeding, and resting is of course sensitive to the level of hunger of the animal and its familiarity with the arena.

Salomone (1988) has demonstrated that effective behavior switching in a similar environment is compromised by the dopamine antagonist Haloperidol and by dopamine-depleting lesions of the striatum.

Figure 10. The behavior of an adult rat in this square arena with a shaded nest area (top right) and central food resource has provided the inspiration for an embodied model of action selection in the vertebrate basal ganglia.

Our recent efforts have focused on producing a similar, if much simplified, problem setting for a *Khepera* mobile robot and have resulted in the following model:

The wheeled robot, which possesses a gripper-arm and a ring of infra-red distance sensors, is placed in a square, walled arena in which a number of small cylindrical objects are also placed. The cylinders substitute for food pellets, so the consumption of food is modelled by collecting cylinders and depositing them in the corners of the arena. The robot has five action sub-systems which it can switch between at any time, these are *cylinder-seek, cylinder-pickup, wall-seek*, *corner-seek*, and *cylinder-deposit*. The 'salience' of each sub-system at a given moment depends on the values of various *extrinsic* and *intrinsic* variables. Extrinsic variables include *wall-detect*, *corner-detect*, *cylinder-detect*, and *gripper-status*, and are computed by perceptual sub-systems that process the raw sensory data available to the robot. *Intrinsic variables* currently include 'hunger' and 'fear' and are computed by motivational sub-systems as a function of recent behavior and experience. So, for instance, 'fear' is a function of exposure to the environment and is reduced by time spent exploring the environment,

while 'hunger' is a function of time and collecting cylinders and is reduced when cylinders are deposited in the corners of the arena. At each time-step these variables are provided to the input (striatum) components of the model basal ganglia which compute a *salience* value for each behavior as a weighted function of the variables relevant to that behavior. The intrinsic circuitry of the basal ganglia model then resolves the competition between behaviors and disinhibits the motor output of winning action sub-systems. Conflicts arise between the different action sub-systems arise for several reasons: first, the *extrinsic variables* are affected by significant sensor noise; second, 'fear' increases the salience of the *corner-seek* and *wall-seek* sub-systems; and third, 'hunger' increases the salience of the *cylinder-seek* sub-system. Thus, depending on circumstances, two or more action sub-systems can have significant, possibly similar, levels of salience at any given time.
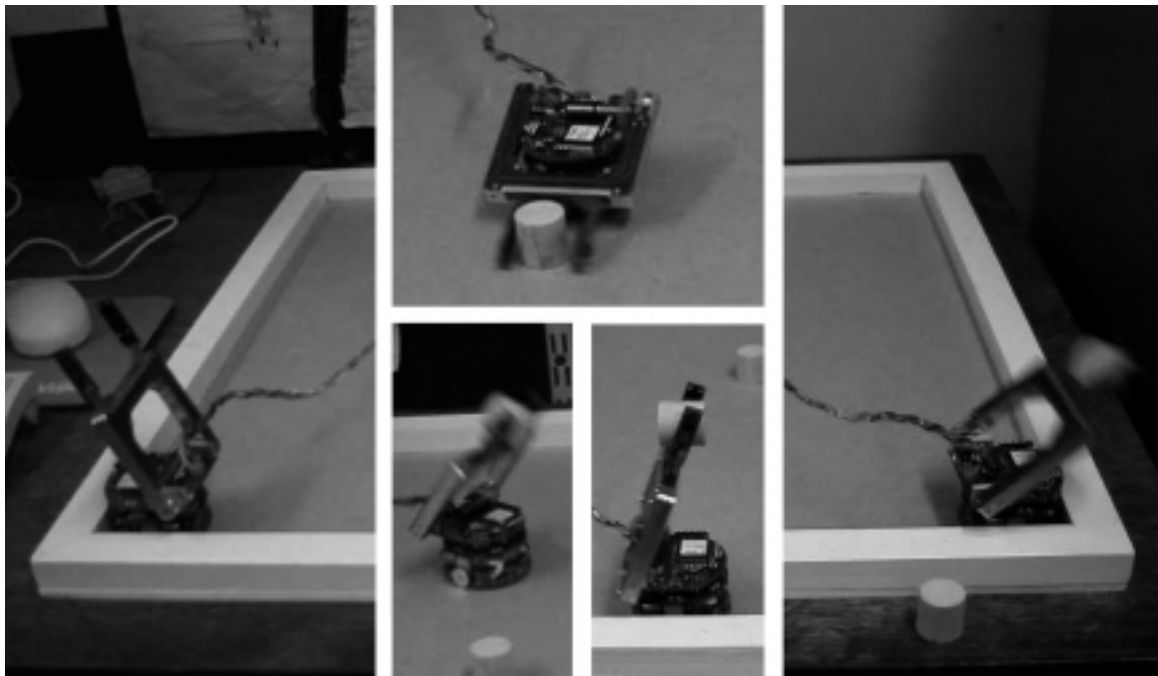

Figure 11. The behavior of the robot model. The photographs show the robot searching for cylinders (left*),* picking up a cylinder (center, top), look for a wall (center, bottom, left), look for a corner (center, bottom, right), and depositing the cylinder in a corner (right).

Our initial experiments (described in greater detail in Montes Gonzalez et al., 2000) have demonstrated appropriate and clean switching by the embodied basal ganglia. In other words, the robot selects appropriate actions for different circumstances and generates sequences of integrated behavior. Snapshots of such behavior are shown in figure 11. Of course, this is not a particularly impressive achievement in terms of robot control—alternative and certainly simpler control architectures could be as effective in performing these simple tasks. Nevertheless, this result does provide an important demonstration that the proposed basal ganglia selection mechanism *is* capable of effective and clean switching when embedded in a 'complete creature'. Initial experiments with simulated dopamine modulation have also generated

encouraging results. For instance, lowering dopamine below the normal tonic level causes the robot difficulty in approaching a cylinder (to be picked up), or in releasing one that is currently held. Furthermore, in a reduced dopamine condition, a selected action sub-system may not always be fully disinhibited resulting in the desired movement being performed more slowly than is normal. There may be an interesting similarity between the slowing of movement observed in the robot and the bradykinesia observed in human patients with Parkinson's disease. We hope that future experiments will show further specific similarities between behavior switching in the model and in vertebrates. Of course we are currently a very long way from modelling the much richer behavior of the rat shown in figure 10, however, we believe we have made a start.

6   Conclusions: the evolution of action selection

We have provided a brief review of the neural substrate of action selection in a number of living animal groups. The particular animals we have considered were chosen to reflect an evolutionary trajectory that leads from the very first nervous systems to those of the vertebrate class to which we ourselves belong. Of course, this path leaves out the vast majority of living animals including all the advanced protostome invertebrate classes, such as the insects, that have provided such valuable inspiration to recent research in robotics. The wider study of the evolutionary neurobiology of both protostome and deuterostome phyla should provide evidence of convergence and divergence in control system design that may help in the search for 'forced moves' or 'good tricks' (Dennett, 1996) in the design space for autonomous mobile beings. For instance, evolutionary convergence (where two animal groups show similar acquired solutions to a control problem, and the same solution is not observed in their common ancestor) suggests either strong task constraints (a 'forced move' in design space) or the existence of a robust, and relatively general solution to a common problem (a 'good trick'). Our review has also been limited to discussing neural circuits although there is good evidence that other mechanisms, such as the endocrine system[6], can play an important role in action selection (see, e.g. Barrington, 1967; Brooks, 1994). Despite these limitations, we believe that a number of conclusions can be drawn from the findings we have surveyed.

First, the investigation of cnidarian nervous systems shows that many forms of behavioral integration can be achieved in complex multi-celled animals in the relative absence of centralised nervous system structures. The elegance of these natural

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[6] It is interesting to note in this regard, that the first nerve cells may have been neurosecretory, in other words, diffuse chemical signalling may have preceded electrical conduction in the evolution of animal control systems (Horridge, 1968; Mackie, 1990).

solutions is only just beginning to be matched by those developed for distributed robot control systems. We suspect that the study of cnidarian nervous systems and behavior could provide many useful ideas for the design of future 'minimalist' mobile robots.

Second, our review of flatworm nervous systems suggests that the evolution of centralised selection mechanisms in the archaic brain may have been a prerequisite for maintaining behavioral coherence in a bilaterally-organised animal. The value of a centralised action selection circuit in an otherwise distributed and behavior-based architecture has been recognised by Rosenblatt and Thorpe (1995) in their design for a mobile robot control system. More generally, it seems likely that the design of artificial control systems could benefit from the use of centralised conflict resolution systems because of the advantages that this form of modularity can confer (see Prescott et al., 1999; Bryson, in Press).

Finally, our review of the neural substrate of action selection in vertebrates has identified a number of candidate selection mechanisms that may be instantiated in their neural circuitry. A key proposal is that the vertebrate nervous system exploits specialized switching circuitry found in a group of central brain structures called the *basal ganglia*. We have briefly described the functional architecture of this circuit, showing that it could support effective switching, and have reviewed evidence demonstrating behavioral disintegration in animals with basal ganglia damage. We have also outlined some initial progress in developing a robot control system designed around a 'basal ganglia' selection circuit. It seems possible that the connectional economy of the basal ganglia, which could arbitrate between functional sub-systems distributed widely in the brain, may be one the reasons that the vertebrate nervous system has scaled successfully with the evolution of animals of larger brain and body size.

Although we believe the basal ganglia to be an important component in vertebrate action selection it is only one of many mechanisms subserving behavioral integration in the vertebrate brain. For instance, we know from studies of infants rats, in whom the basal ganglia are not yet developed (see, e.g. Berridge, 1994), that there must be a 'scaffold' of alternative selection mechanisms that can provide appropriate behavior switching while the adult architecture is developing. We have also noted partial recovery of behavior switching following major basal ganglia damage. This, together with the evidence we have cited for conflict resolution circuitry elsewhere in the vertebrate brain, supports the existence of multiple substrates for action selection in the vertebrate nervous system. Action selection as the emergent consequence of interactions between circuits with wider functional roles may also be important in vertebrates, although, by its very nature, this form of switching will always be difficult to demonstrate empirically.

The design of control systems for robots with multiple actuator sub-systems should benefit from understanding how the vertebrate nervous system maintains behavioral coherence. The current analysis of action selection in the vertebrate brain suggests that specialised conflict resolution mechanisms could play an important role in the control of the 'whole iguana' and also, perhaps, in its robotic counterpart.

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