COMMENTARY

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

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Abstract—A *selection problem* arises whenever two or more competing systems seek simultaneous access to a restricted resource. Consideration of several selection architectures suggests there are significant advantages for systems which incorporate a central switching mechanism. We propose that the vertebrate basal ganglia have evolved as a centralised selection device, specialised to resolve conflicts over access to limited motor and cognitive resources. Analysis of basal ganglia functional architecture and its position within a wider anatomical framework suggests it can satisfy many of the requirements expected of an efficient selection mechanism.

Key words: behaviour, action, movement, switching, model, architecture, motor control

INTRODUCTION

Despite a prodigious volume of work in recent years there is still no consensus concerning the computational operations performed by the basal ganglia. Indeed, there is evidence linking the basal ganglia to an extensive range of processes including perception[9], learning[28], memory[56], attention[48], many aspects of motor function[34, 59,73], even analgesia[17] and the suppression of epileptic seizures[23]. To accommodate the rapidly accumulating wealth of information, there is a pressing need to develop clear and testable hypotheses concerning the computational role(s) of the basal ganglia. This commentary seeks to promote one such simplifying theory by exploiting one of the recurrent ideas in basal ganglia literature—that the essential role performed by the basal ganglia is *to select some actions/motor programmes at the expense of others*[5,18,22,37,65,73,81,94,95].

An increasingly successful approach to the understanding of brain function is to combine the "top-down" analysis of a behavioural problem faced by the organism, with the "bottom-up" analysis of the operation of the nervous system[3]. The top-down approach establishes the computational constraints of the task to be solved and suggests some of the organisational principles that might help us to interpret observed characteristics of neural circuitry. The bottom-up approach stems from neuroanatomical, neuro-chemical, electrophysiological, and neuro-behavioural analyses, and provides clues as to how a given control problem may be decomposed and implemented by the brain. The two approaches can inform, motivate, and refine each other, leading, it is hoped, to an eventual understanding that is consistent across both levels. In this commentary we consider a top-down analysis first, drawing on ideas from ethology and cybernetics to identify and characterise the selection problem faced by an autonomous being (be it animal or robot). We then look from the bottom-up at what is known of the physical characteristics of the basal ganglia, and attempt to find in this neural circuitry an

architecture that could implement the selection task. Finally, we briefly consider how the proposal that the basal ganglia act primarily as a selection device could substitute for the multiplicity of functions currently suggested for these structures.

A GENERAL PROBLEM

A *selection problem* arises whenever two or more competing systems seek simultaneous access to a restricted resource. For example, in a vertebrate or in a robot, multiple sensorimotor systems may require access to the limited resource that is the final common motor path. Detectors of targets to-be-acquired must share arms/legs/wheels with detectors sensitive to threats to-be-avoided. Effective behaviour requires that conflicts between activated systems requesting in-compatible actions are resolved appropriately and rapidly. Conflicts can also arise in domains where behavioural expression is more indirect, for instance between systems competing for access to limited cognitive resources. The theory to be advocated here is that the basal ganglia has evolved to resolve conflicts over access to limited motor and cognitive resources by selecting between competing systems.

The problem of selecting between behavioural alternatives has a long history in the ethology literature where it is termed the problem of 'behaviour switching' or 'decision-making'[62]. More recently it has emerged as a practical issue in the control of mobile robots[8] and other artificial agents[58] where it is often termed the 'action selection problem'[71]. Differences in terminology partly arise because selection can occur at different levels of a control system and on different time-scales. Here we will consider aspects of the generic selection problem first, we will then consider issues arising from the need to make multiple parallel selections, and the possibility of multiple levels of selection within a complex control system such as the brain. We will reserve the term *switching* to denote the tran-sition of control from one selection to another.
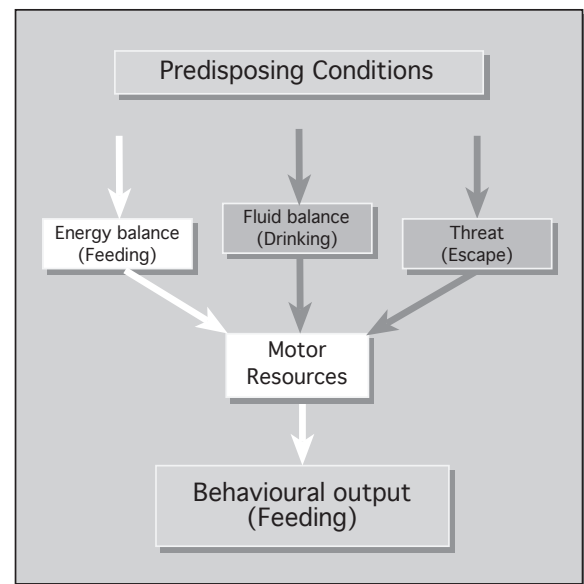

Fig. 1. A mechanism is required to ensure that parallel processing behavioural systems which are mutually exclusive have orderly access to limited motor resources—the final common motor path. The density of shading (lighter = high levels of activation) indicates that the selection problem should be resolved on the basis of 'winner-take-all'.

Selection and switching

Consider a hypothetical and simplified animal with three behaviours—feeding, drinking, and escape—which we assume to be mutually exclusive (Figure 1). Clearly the urgency or *salience* for any one behaviour, say feeding, should depend on a variety of *causal factors* both *extrinsic* to the animal (such as the presence of food stimuli) and *intrinsic* (such as the current level of energy reserves). When the level of causal factors for feeding is high we should expect the animal to eat, however, we should expect that feeding will give way to drinking if the latter need becomes more pressing. The animal might also switch from feeding to drinking as it becomes increasingly satiated, or if it is un-successful in obtaining food. Since survival is a priority for any animal, we might also expect the presence of even a relatively weak threatening stimulus to cause a rapid switch from either eating or drinking to escape. Finally, in a changeable environment, it would be beneficial for the overall balance between behaviours to be adaptable. Thus selection criteria (relative saliences) should be determined partly through inherited features of the

relevant neural circuits, and partly through learning from experience.

The above example captures many of the essential features of the generic problem of selecting between multiple incompatible com-petitors. In general terms, we can say that the salience of each competitor should depend on the relevant causal factors for its expression which can be both extrinsic and intrinsic to the control system. Selection should then depend on the relative salience of the competitors, weighted so as to provide appropriate dominance relation-ships, and adaptable to cope with a non-stationary world. Our hypothetical example also suggests the circumstances under which a switch between competitors should take place. A selection should be terminated when its expression has been successful or if it proves to be ineffective. It may also be *interrupted* by a competitor with a higher level of support.

In addition to these computational requirements for selection we can identify a number of desirable characteristics for effective switching. First, a competitor with a slight edge over the rest should see the competition resolved rapidly and decisively in its favour so providing *clean switching*. Second, the presence of competitors that are activated but not engaged should not interfere with expression of the winner's outcome once the competition has been resolved; this can be termed absence of *distortion*. Both these properties can be provided by mechanisms that implement 'winner-take-all' functionality[84,94]. We may expect, therefore, to find circuits with winner-take-all properties involved in biological action selection. Following selection, a winning outcome may begin to reduce the salience of its predisposing conditions (as these become partially fulfilled). When the salience falls below that of a close competitor a switch may then take place. The same can happen with this second selection, however, causing a switch back to the first competitor, and so on. This phenomenon, whereby a selector oscillates between two closely matched competitors, is termed *dithering* and can be resolved by endowing the switching mechanism with some form of *persistence*[62], (also termed *"hysteresis"*[84]). An effective way to introduce persistence into a switching circuit is to incorporate

a non-linear positive feedback loop which maintains, or momentarily enhances, the support for the winner.

Multiple selections and the need for different levels of control

Animals can be viewed as control systems with multiple output channels. In principle, each channel could be controlled independently—it is typically *not* the case that when a competition for use of one set of muscles is resolved, access to all other muscle groups is automatically denied. Thus, with few exceptions, most of us can actually walk and chew gum! The independent control of multiple channels therefore suggests the need for multiple selection mechanisms each arbitrating between a pool of competitors bidding for incompatible uses of a given channel.

Having provided conflict resolution within each channel, one option would be simply to allow separate output systems to 'do their own thing'. However, such a scheme has the obvious potential for simultaneous activation of outputs which although compatible are *inappropriate* with regard to either the well-being or higher-level objectives of the animal. For instance, it is generally unwise to persist in walking forwards while looking backwards. The need for appropriate combinations applies both to simultaneous and sequential activity of output systems. There is therefore a clear requirement for at least one additional higher level(s) of control which can decide between appropriate and inappropriate combinations of lower level selections.
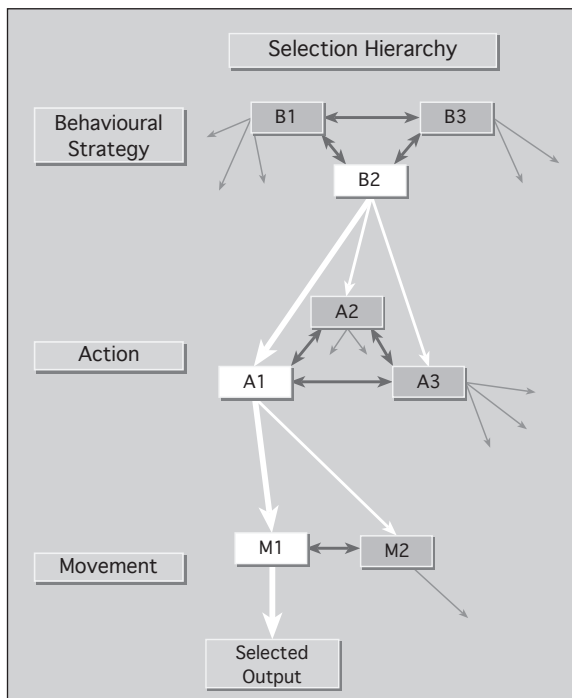
Fig. 2. Hierarchical decomposition of the selection problem. Again levels of activity within different components are represented by density of shading; light = high activity. The dark arrows at each level represent reciprocal inhibitory connections which would support "winner-take-all" selection between elements. Selections at the highest level determine overall behavioural objective (B1-3). Activated connections (white arrows) from the selected/winning element (B2) represent priming signals to lower level components associated with that element. Grey arrows represent non-activated priming signals from non-selected/losing elements. At intermediate levels, action (A1-3) which can achieve higher level objectives is selected (A1) . At the lowest levels (M1-2) selection enables a pattern of motor activity (M1) which can produce the selected action.

The ethological and neurobiological analysis of behaviour suggests there are indeed multiple levels of selection within the vertebrate nervous system[29]. A commonly adopted functional decomposition of selective processes is illustrated in Figure 2. At the highest level, selections are required that decide the current general course of action. At intermediate levels, selection specifies appropriate patterns of co-ordinated movements in the context of the current high-level aim. Finally, at the lowest levels, selection determines patterns of appropriate muscular activity that can deliver the currently selected action. This hierarchical decomposition of selection makes decision-making a tractable enterprise since, at any given moment, it restricts lower-level competitions to just those competitors capable of implementing current higher-level objectives. Because many aspects of the selection problem are the same at all levels, copies of a standard selection circuit, provided with appropriate input/output connections, could be used to resolve disputes at multiple levels.

SELECTION ARCHITECTURES

A variety of architectures have been proposed to deal with the selection problem in both artificial and biological systems[58,62,8,84]. Some of these will now be described and considered as possible templates for interpreting patterns of connectivity that could implement selection within the vertebrate brain.

A robust architecture to control the behaviour of autonomous mobile robots has been developed by Brooks[8] (Figure 3A). Termed the 'sub-sumption architecture', it consists of a hierarchically organised set of layers. Each layer has a specialised sensory input linked to motor output that generates a specific behavioural competence. Higher layers implicitly rely on the appropriate operation of those below. In the subsumption architecture conflicts between layers are handled according to a fixed priority scheme. Higher layers can 'subsume' lower ones, principally by inhibiting their outputs and (optionally) substituting their own, however, lower layers do not have the reciprocal ability to interrupt or suppress the outputs of those above. Layered architectures of this type allow rapid responses to environmental contingencies and can provide appropriate action selection for robots with a limited number of behavioural goals. However, since prioritisation is 'designed-in', it becomes difficult to determine an ap-propriate dominance hierarchy as the control system is made more complex[8]. While the characteristic organisation of subsumption architectures bears a number of interesting similarities with biological nervous systems[71], current evidence suggests that selection in adult vertebrates is implemented in a more flexible manner than a purely hierarchical selection system will allow[29].
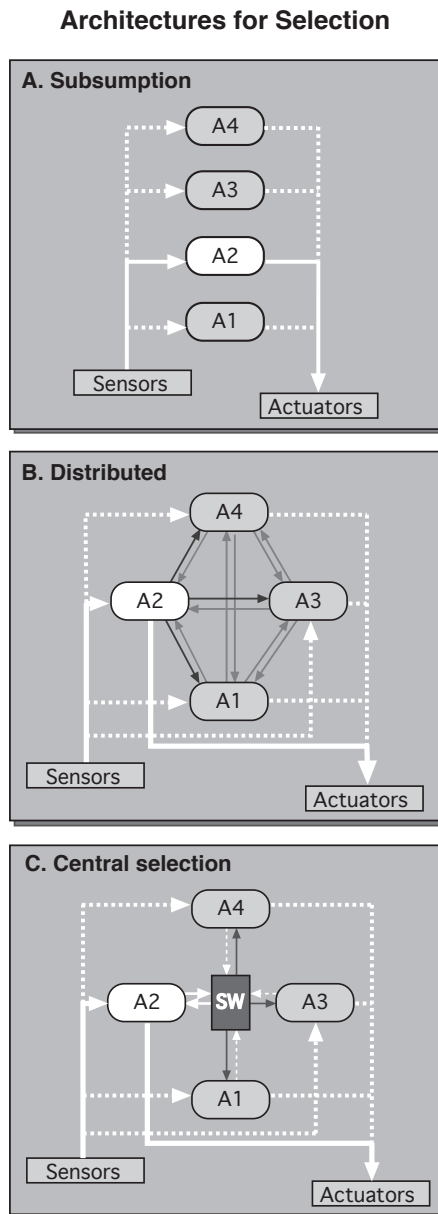
Architectures for Selection

Fig. 3. Architectures proposed to solve the selection problem. **A**. A hierarchical 'subsumption' architecture 8 in which disputes between actions (A1-4) represented in different layers are resolved by a pre-programmed fixed priority scheme. **B**. A 'distributed' network in which each competing module (A1-4) has a reciprocal inhibitory connection with every other and an excitatory link to the shared output resource. Solid white arrows represent greater support for A2 which in turn imposes greater reciprocal inhibition on competing elements (black vs grey arrows). **C.** A central selection mechanism can be used to determine access to the shared output resource with fewer connections. Note the central switch (SW) detects greater support for element A2 and provides return facilitation for this element (white arrows); less well supported ('losing') elements are inhibited (dark arrows) by the central switch.

A second class of *distributed* selection architectures is illustrated by the network shown in Figure 3B. In architectures of this type all competitors are reciprocally connected so that each one has an inhibitory link to every other—an arrangement termed *recurrent reciprocal inhibition*[27,94]—and an excitatory link to the shared output resource. Such networks display a form of positive feedback since increased activity in one competitor causes increased inhibition on all others thereby reducing their inhibitory effect on the first. Recurrent reciprocal inhibition can therefore support winner-take-all functionality making it an attractive means for implementing action selection. The relative strengths of incoming excitatory links, and of the inhibitory links between competitors, can also be tuned to support a complex pattern of dominance relationships so that over an extended period, resource allocation among the competitors can be optimised. Reciprocally inhibiting networks are widespread in the central nervous system[29,98] (including the basal ganglia - see below), however, connection costs are likely to preclude it from being the direct arbiter of selection between functional units distributed widely throughout the brain. Specifically, it has been noted[63] that to arbitrate between *n* competing behaviours, a fully connected network with reciprocal inhibition requires *n(n-1)* connections; to add a new competitor requires a further *2n* connections. Reciprocally connected architectures are there-fore high cost both in terms of the density of connections between rivals and in the cost of integrating a new competitor into an existing network. Insofar as neural activity incurs a high metabolic debt, evolution should normally prefer architectures which achieve comparable functionality with fewer connections, lower levels of activity, and are more easily augmented in a modular fashion.

The distributed architecture just described provides a good example of a control system in which there is no central switch device, indeed, selection of one competitor over another is often described as an *emergent* property of the net-work[58,84]. More generally, there are many examples of biological and artificial systems in which switching between alternative modes of operation arises through dynamical properties of the circuitry in such a way

that it is difficult or impossible to identify circuit components that are exclusively involved in selection. For instance, investigations of invertebrate neural circuitry have identified multi-functional pattern gener-ators that can be driven by relatively small changes in input (or in neuromodulatory substances) to switch from one behavioural output to another[32]. The components of these circuits that are involved in behavioural switching cannot be easily distinguished from those involved in other functions such as motor control. It has been suggested that vertebrate pattern generators may exploit similar forms of distributed or emergent switching[53]. In general therefore, it seems likely that the selection that occurs in various functional sub-systems within the vertebrate brain could be of a distributed or emergent nature.

There are, however, good reasons why both artificial and biological control can benefit by exploiting *centralised* selection mechanisms for overall behavioural control (Figure 3C). Following McFarland[63], Snaith and Holland[84] contrasted a distributed selection network with one which employed a specialised selection device (compare Figures 3A and 3B). They pointed out that an architecture with centralised selection requires only two connections for each competitor (to and from the selection mechanism) resulting in a total of *2n* connections. This is a considerable saving over the *n(n-1)* connections required by the dist-ributed architecture. Moreover, to add a new competitor to the central selector only two further connections need be incorporated compared to the *2n* required for reciprocal inhibition between all competitors.

A second argument in favour of specialised selection circuitry derives from the general argument for modularity in the design of control systems. Insofar as the problem of selection can be distinguished from the perceptual and motor control problems involved in co-ordinating a given activity, it should be advantageous to decouple the selection mechanism from other parts of the control circuitry. Thus, each separate component could be improved or modified independently. By contrast, in a circuit that displays emergent selection, a change directed at some other aspect of function could impact on the switching behaviour of the

network with possibly undesirable consequences. The advan-tages incurred by modularity in dissociating functionally distinct components of the system are probably as significant for evolved systems as they are for engineered ones[89].

In addition to the requirements for appropriate selection and effective switching identified above, we can add a number of further constraints which apply particularly to the design of a central selection mechanism arbitrating between multiple competitors. First, the device requires appropriate inputs that can indicate the status of the different causal factors for each competitor. Second, it must be possible for the salience of all competitors to be determined in some *common currency* that allows their relative levels of support to be compared[62]. A simple and widely-used heuristic is that after causal factors and dominance have been factored in, the most strongly supported competitor should be preferred[62]. Third, the outputs of the selection device should be appropriately connected so as to enable the expression of the winning competitor while disabling that of the losers.

THE VERTEBRATE SOLUTION?

We propose that the basal ganglia provide the vertebrate brain with a specialised, central selection mechanism to resolve conflict between competing systems at different functional levels (Figure 3C). To support this assertion we will identify characteristics of basal ganglia circuitry that match each of the requirements hitherto identified for such a device. We will also suggest that distributed selection mechanisms (Figure 3B) are employed *within* basal ganglia circuitry in a manner that exploits their useful switching properties whilst minimising the undesirable overheads incurred by reciprocal inhibition.
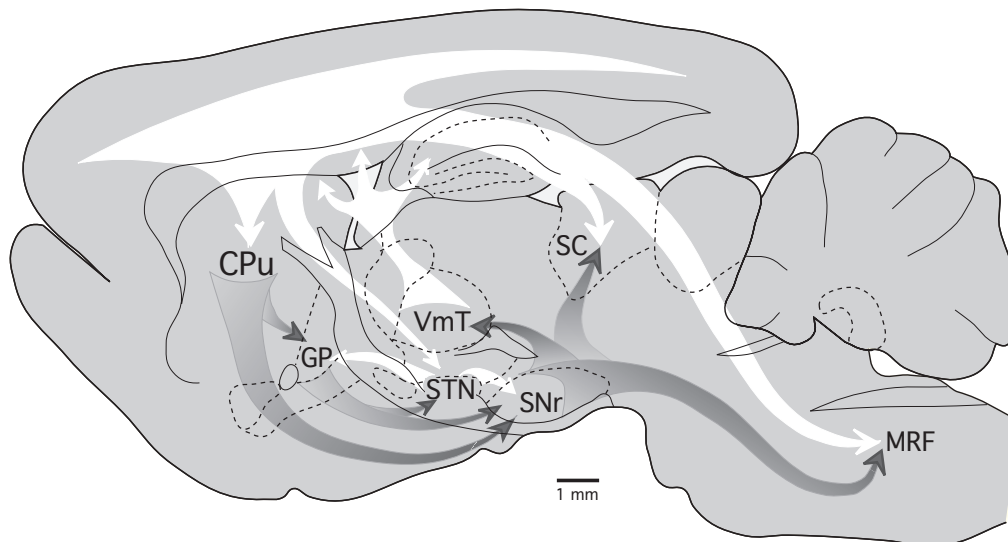
Fig. 4. A selected representation of basal ganglia connectivity illustrated on a parasaggital section of rat brain (Lat. 2.4mm). Excitatory connections are illustrated in white, inhibitory ones are shown in black. To avoid a confusing proliferation of arrows, input connections are limited to cortical projections to the caudate/putamen (CPu) and subthalamic nucleus (STN), intrinsic connections between the CPu, globus pallidus (GP), substantia nigra pars reticulata (SNr) and the STN, and output connections from SNr to the ventromedial thalamus (VmT), the superior colliculus (SC) and the medullary reticular formation (MRF).

It is important, at this point, to emphasise that we are not suggesting the basal ganglia have a monopoly on selection in the vertebrate nervous system. Indeed, it is likely that selection, at one level or another, occurs throughout the brain, much of it distributed with emergent properties. However, where there is a specific need to arbitrate between functional units that are widely distributed, it is clear that a central selection device could play an important role. It is our contention that this is the core function of the basal ganglia. However, before considering how particular features of the basal ganglia might satisfy general requirements of a selection architecture, we will first provide a brief overview of their functional anatomy.

OVERVIEW OF BASAL GANGLIA FUNCTIONAL ANATOMY

There have been many excellent recent reviews of the functional anatomy and neurochemistry of the basal ganglia[31,65,95]. We shall therefore focus primarily on those aspects which are relevant to their potential role in selection (Figure 3C). Selected components of the basal ganglia are therefore illustrated in Figure 4. They include the striatum (caudate nucleus, the putamen and ventral striatum), the subthalamic nucleus, globus pallidus and substantia nigra.

The principle *input* components of the basal ganglia are the striatum and the subthalamic nucleus. Afferent connections to both structures originate from virtually the entire cerebral cortex (including motor, sensory, association and limbic areas), from the midline and intralaminar nuclei of the thalamus, and from the limbic system (principally the amygdala and hippocampus). These connections are excitatory, intermittently active, and use glutamate as a neurotransmitter.

The main basal ganglia *output* nuclei are the substantia nigra (pars reticulata and lateralis) and the entopeduncular nucleus (internal segment of the globus pallidus in primates). These structures provide extensively branched efferents to the thalamus (which in turn projects back to the cerebral cortex), and to pre-motor areas of the brainstem including superior colliculus, inferior colliculus, periaqueductal gray, pedunculo-pontine/ cuneiform area, and widespread regions of the mesencephalic/medullary reticular form-ation. Most output projections are tonically active, inhibitory and use GABA as a neuro-transmitter.

The *intrinsic* connections of the basal ganglia are organised so that phasic input can either decrease or increase the tonic inhibitory effect of the output nuclei on their target structures. Thus, direct inhibitory connections between one neurochemically defined population of striatal cells and the output nuclei suppress tonic output firing, and thereby disinhibit targets in the thalamus and brainstem. Via a second point of entry, external afferents to the subthalamic nucleus (which projects directly via excitatory connections to the output nuclei), can increase the level of tonic inhibitory control over the thalamus and brainstem. The globus pallidus receives inhibitory input from a second neurochemically defined population of striatal neurones, and excitatory input from the subthalamic nucleus. Tonic inhibitory output from the globus pallidus branches back to the striatum and the subthalamic nucleus, and forward to the basal ganglia output nuclei. The role of these connections in modulating basal ganglia output is at present, however, poorly defined. Further intrinsic processing is provided by dopaminergic projections from the ventral midbrain (substantia nigra pars compacta and ventral tegmental area) to the striatum (not illustrated in Figure 4). Mesencephalic dopamine cells in turn receive a direct inhibitory projection from the striatum (predominantly from neuro-chemically defined patch/striosome compart-ments of the striatum[31]) and an excitatory input from the subthalamic nucleus[66].

Within this general anatomical framework there are additional features which may have special significance for the proposed role of selection. For example, there is a growing consensus that the basal ganglia nuclei can be regionally subdivided into functionally segregated territories (skeleto/oculomotor, associative, and limbic) depending on their topographically organised patterns of connectivity with each other and with cortical and thalamic regions having the same functional subdivisions[1]. Thus, current views of information processing within the basal ganglia are heavily influenced by the suggestion of *multiple parallel channels*. These channels originate in the cerebral cortex, project via topographically segregated pathways through the basal ganglia nuclei, and return via a thalamic relay to the region of cortex from which the specific cortico-striatal projections originated[86]. However, a growing body evidence points to the presence of open-loop as well as closed-loop projections where some outputs return to cortical locations other than their site of origin[51].

A further pattern of organisation has been identified within the motor domains of the basal ganglia. In the lateral striatum of rodents, and in putamen of primates, the individual parts of the body which play the most active roles in movement are represented somatotopically[11]. Thus, cells with sensory or motor specificities associated with a specific musculature (e.g. hindlimb, forelimb, oral or oculomotor) are found in localised regions of the striatum[10,26]. Selective inactivation or damage to these areas produces impairments in tasks which involve using that particular body part [70].

We will now argue that the anatomical architecture of the basal ganglia is consistent with a primary role of a central selection device. We focus first on evidence, drawn primarily from the motor domain, that the circuitry of the basal ganglia is well-suited for the task of selecting between multiple, incompatible movements. Thereafter, we attempt to generalise this view to cover multiple levels of selection and to selection in both the motor and cognitive domains.

A GENERAL MODEL OF ACTION SELECTION BY THE BASAL GANGLIA

In the vertebrate brain, functional systems capable of specifying action, (henceforth *command systems*[24]), are likely to be distributed throughout all levels of the neuraxis. Since multiple command systems can operate in parallel, a clear problem concerns the allocation of restricted motor resources between competing demands. We propose that the channelled architecture of the basal ganglia could provide the solution to this problem. Figure 5 provides an overall plan of how centralised selection in the basal ganglia could combine with other functional units to determine access to limited motor resources. We will now consider the major components of this model.
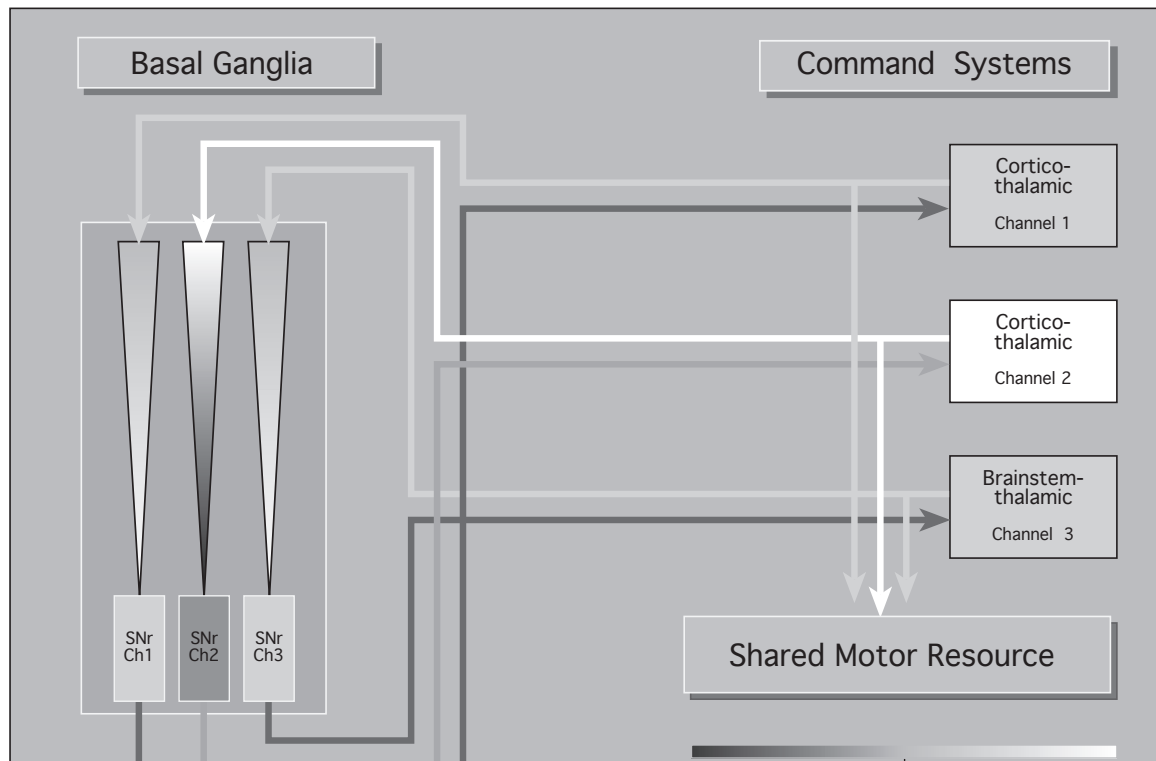
Fig. 5. A conceptual model of selection by the basal ganglia between three command systems (Channels 1-3) competing for access to a shared motor resource. In this model excitatory connections are represented by light grey–white and inhibitory ones by dark grey–black. The lightness and darkness of the components relative to the background represent differing levels of excitatory and inhibitory activity. The model assumes that the internal circuitry of the basal ganglia (not shown) is configured so that, at the level of the output nuclei (e.g. SNr - substantia nigra pars reticulata), selected channels are inhibited while non-selected channels are excited[65, 94]. Because of the inhibitory nature of basal ganglia output, targets of selected channels will be disinhibited [16] while inhibition on non-selected channels is maintained or increased. In this manner activity in the most actively supported (salient) command system will be sustained and its direct links with the motor plant unblocked. Conversely, less well supported command systems will be inhibited and their access to the motor plant denied. The components of this model share essential features with the anatomical connectivity illustrated in Figure 4 and the central switching circuit illustrated in Figure 3c.

A common feature of all the selection mechanisms illustrated in Figure 3 is that the competitors which initiate and subsequently guide actions have direct connections with the output systems that deliver motor behaviour. This also appears to be the case in the vertebrate brain. A wealth of anatomical evidence shows that command systems at all levels of the neural hierarchy communicate directly with cortical and/or hindbrain pre-motor and motor mech-anisms[12]. We will refer to these target motor systems collectively as the *motor plant*. For the purpose of illustration we have included just three competing command systems with direct connections to a shared motor resource (Figure 5). In the centralised selection model (Figure 3C) all competitors have connections to a shared conflict resolution device. Afferent projections to the striatum from the brainstem (via the thalamus), limbic system and most regions of cerebral cortex suggest the basal ganglia may be uniquely connected with a wide range of potential command systems. We have represented inputs to the basal ganglia as branching connections from the main communication lines between command systems and motor plant (Figure 5). While this branching architecture appears to be common (see below) it may not be a necessary feature of all striatal afferents[68]. However, it is important for the model (Figure 5) that at least one class of input to the basal ganglia conveys signals related to the urgency or *salience* of the different competing commands. Evidence for this sug-gestion is considered below.

The selection mechanism must be able to resolve the competition between incompatible inputs. Although we have a working quantitative stimulation which contains a representation of internal basal ganglia circuitry (Gurney et al. in preparation) and selects effectively between competing inputs, in Figure 5 we have left the means by which specific input channels achieve priority unspecified. A general understanding of the model can however, be gained by assuming that internal circuitry may be configured to select the most salient inputs on a winner-take-all basis[94] and, at the level of the output nuclei (SNr in Figure 5), selected channels are inhibited while non-selected channels are excited.

Finally, through appropriate outputs, the selection device must enable connections between the winning command generator(s) and the motor plant whilst simultaneously denying access to the losers. The tonic inhibitory output from the basal ganglia to multiple targets in the thalamus and brainstem[16] acts to block the direct connections between command systems and the motor plant. Following the suggestion of others, our model assumes that focused disinhibition of a selected channel[65,95], would remove the tonic inhibitory block selectively from the winner's direct communications with the motor plant. In this manner, restricted access to the motor system could be allocated, at any given time, to the most salient/urgent command. We will now expand on some of the key proposals in this model and examine the extent to which its operation could meet the requirements for efficient conflict resolution outlined above.

Branched pathways from command systems to basal ganglia and motor plant

Modern tract tracing technology has provided increasing support for the view that much of the input to the basal ganglia comprises relatively fine collateral branches emanating from larger fibres projecting to motor regions of the brainstem and spinal cord, the thalamus or other regions of the cerebral cortex[55,97]. In the case of subcortical command systems, it is probable that branched projections to the brainstem motor plant and basal ganglia are made via a link in the thalamus. For example, output neurones in the intermediate layers of the superior colliculus which have direct contact with regions of the contralateral brainstem involved in orienting behaviour, also have an ascending branch to the intralaminar and parafascicular thalamic nuclei[15], which in turn project directly to the striatum[4,87]. In the light of such observations it has been suggested previously that the striatum could receive copies of cortical commands sent directly to the motor plant[31,97]. From the point of view of the current model, it will be important to establish what aspect(s) of these signals is extracted for processing by the basal ganglia.

A common input currency?

If copies/correlates of action commands are relayed to the basal ganglia to compete for selection, we noted above that a likely requirement for efficient selection is that the most strongly supported input should prevail. This means that there must be a feature of the command signal, common to all competitors, which can be directly compared and used as a basis for selection. An interesting possibility for a *common input currency* for action selection is contained in the *dual population coding* model of cortical signals reported recently by Koechlin and Burnod[54]. In this model, signal attributes are encoded in terms of the distribution of cell activity within a population of neurones (the 'landscape' of neural activity), while the salience of the signal is coded in terms of the overall intensity of firing within the population. In this way, both the meaning of an item of information *and* its significance for the brain can be encoded in the same population response. Support for the view that the size of population vector may denote salience (rather than other command attributes) comes from studies of monkey motor cortex where vector size has been found to influence the decision of when, rather than where to move[30]. Since there is evidence for population coding throughout the brain[54,85], a rep-resentation of overall levels of activity in competing command systems could be made available, via the connections mentioned above, to the input nuclei of the basal ganglia. Here, 'winner-take-all' selections could be made on the basis of salience differences between the competing inputs.

Contextual and evaluative inputs to the basal ganglia

It is unlikely, however, that all afferents to the basal ganglia represent the salience of competing command systems since a range of evidence indicates the presence of several qualitatively different inputs.[31]. One possibility is that a wide variety of contextual information is made available to the striatum[38,79] which could serve to either enhance or reduce the salience of 'command-related' inputs. Anatomical[31] and electrophysiological data[25] certainly indicate that potentially co-operative influences from diverse sources converge on striatal input cells. While it is possible to envisage circumstances where a population response in a single command system would be sufficient to attract selection (e.g. orienting to sudden novel stimuli), synchronised convergence of multiple contextual inputs[97] may be an adaptable method for boosting the 'input' salience of a particular command in a specific situation. It is also likely that information related to the progress of selected actions (success or failure) and/or their reinforcement value would be made available to the basal ganglia to ensure appropriate termination of selected actions, and for modifying future selections on the basis of experience.

Appropriate dominance relationships

In any multi-tasking system it is important to ensure an appropriate distribution of shared resources between the different competitors over time. For example, in mammals, 'house-keeping' tasks such as regular grooming must at some stage acquire sufficient salience to gain priority over what may appear to be more urgent pressures[62]. Similarly, it must be assumed that the salience of physically weak stimuli representing a possible threat must be amplified, in part by context, sufficiently to interrupt a current selection and ensure that defensive responses 'win' a subsequent re-prioritisation. The relative strength of different inputs under various stimulus conditions is likely to have been sculpted for the species by the evolutionary process, and for an individual through reinforcement learning.

Desirable characteristics of a switching mechanism

We noted above that an effective selection mechanism should be able to resolve conflicts rapidly (clean switching), prevent 'losing' competitors from affecting the final output (lack of distortion), and avoid dithering (rapid switching between closely matched competitors). Here we briefly discuss how each of these requirements could be met by mechanisms in the basal ganglia.

Several authors have proposed that *winner-takes-all* computations could be supported by local reciprocal inhibitory connections within the basal ganglia[65,94]. Although the anatomical and neurochemical basis of these connections has yet to be identified[49], functional data at the level of the striatum[10], output nuclei[88] and basal ganglia targets[21] provide evidence for a general ex-citatory centre/inhibitory surround organisation which is characteristic of circuits with some form of reciprocal inhibitory connections (Figure 3B). The presence of such connections would be consistent with a winner-take-all functionality proposed by Wickens[94] and Mink[65]. This arch-itecture would allow fast and decisive switching between inputs to local striatal areas which, given the somatotopic striatal organisation noted earlier, could be competing for a common resource.

A necessary part of clean switching is the *clean termination* of current selections. We propose that this function may be one of the roles served by the direct excitatory input to the subthalamic nucleus. This nucleus receives widespread connections from many brain regions via cortical motor areas and the thalamus[6]. Evidence recently reviewed by Mink[65] and Smith et al.[83] suggests that corollary signals directed to the subthalamic nucleus produce a rapid and diffuse excitation of the basal ganglia output nuclei, prior to the arrival of more focused disinhibitory signals from the striatum[14,76]. This temporary excitatory effect on the output nuclei could dispel the disinhibitory activity associated with current selections and send a brief wave of inhibition to brainstem and thalamic targets of the basal ganglia. The outcome would be to interrupt or pause ongoing actions and establish circum-stances in which a new selection may be more easily imposed[65].

In our model (Figure 5), disinhibition of output connections to brainstem and thalamocortical motor areas acts to unblock the direct connections between winning command systems and the motor

plant. At the same time, maintaining or increasing the tonic inhibitory output on non-selected channels denies the losing command systems access to the motor resource. In this manner, contradictory motor commands which could impair performance are suppressed and *lack of distortion* of the selected action would be ensured. A significant amount of electrophysiological[65], behavioural[61,90] and clinical data[13] suggest that unless tonic inhibitory output from the basal ganglia is removed, effective communication between command systems and motor plant cannot be established. In cases where the disinhibitory process is generally impaired (i.e. all channels are sup-pressed) a state of akinesia results which can be overcome only by particularly salient sensory stimuli [60]. In cases where impairment is partial, restricted 'sensorimotor deficits' are reported[70, 74,90]. Conversely, when basal ganglia outputs are jammed in the 'on' (disinhibited) position it is difficult for animals to suppress triggered sensorimotor systems. For example, local application of muscimol (GABA agonist) to the rat substantia nigra[46] or picrotoxin (GABA antagonist) to the superior colliculus[72], tonically disinhibits collicular neurones. Under these circumstances vibrissal input from the sensory trigeminal system appears chronically connected to the collicular outputs that elicit orienting movements. As a result the animal appears unable to resist orienting to and, if possible, biting any tactile stimulus placed in its whisker field. Such animals also appear unable to habituate to repeated stimuli[20,46]. Compulsive orienting has also been observed in the monkey oculomotor system following similar treatments [39,40].

The problem of oscillating between two activities whose salience is closely matched, has been a focus of considerable research in animal behaviour[62]. The requirement for *persistence* can be met by a non-linear, positive feedback pathway[45]. In our model, the removal of inhibition from a winning command system could, in addition to gating the output to the motor plant, provide feedback which enhances the winner's level of support. At the same time, increased inhibition on losing channels could provide non-selected systems with negative feedback therefore reducing salience. The in-trinsic switching circuitry within the basal ganglia could therefore also be involved in promoting the persistence required to prevent dithering.

Dopaminergic regulation of switching

In the dopamine literature there is an important strand of research suggesting that tonic levels of dopamine neurotransmission play an important role in behavioural switching. Consequently, a variety of treatments which alter levels of dopamine neurotransmission have been shown to affect various aspects of selection and switching in a number of different experimental paradigms[18,75,77]. Depending on the site and nature of the intervention, these effects include changes in the dominance relations between behaviours, reductions or increases in switching relative to controls, changes in the variability of behaviour, and failure to complete behaviours. From such data it is possible to draw the general conclusion that mild to moderate increases in dopaminergic activity tend to facilitate switching while comparable reductions in transmission may retard switching[75]. The mechanisms mediating this role may be related to electrophysiological observations by Schneider and colleagues[78] who showed that acute facilitation of dopamine transmission by amphetamine caused a long-lasting increase in the responsiveness of striatal neurones to afferent inputs, while depletion of striatal dopamine had the reciprocal effect of reducing responsiveness. A general increase in the input sensitivity of the selection device could make it more vulnerable to interruption from competing command systems. This effect might have important clinical implications for understanding some of the switching problems reported in schizophrenia and Tourette's syndrome[7,13]. Operating normally however, the general 'tone' of dopaminergic neuro-transmission could play an important role in regulating the frequency and timing of behavioural selections[73].

Dopaminergic neurotransmission in the basal ganglia may play a further important role in behavioural switching. We have noted above that switching should occur when changing circumstances result in higher salience for a competing command system. Observations suggest that the most effective stimuli for inducing such behavioural switches include novel events, primary reinforcers and previously neutral stimuli that have

become associated with reward or punishment. Insight into the way the basal ganglia responds to these 'competitive interrupts' might be gained by considering the short duration (100-150 ms) excitatory response observed in nigral and ventral tegmental dopamine neurones following the presentation of novel or reinforcing stimuli[80]. These responses occur with a very short latency (50-100ms)[44,80], usually prior to the saccadic eye movements which bring the stimulus onto the fovea [50]. Thus, in addition to the widespread subthalamic activation of basal ganglia inhibitory outputs (see above), a similar short latency, short duration excitatory signal is also made available to the ascending dopamine systems. The timing of this response may be important in view of its likely coincidence with the interruption of ongoing behaviour and re-prioritisation favouring orient-ing movements directed to the source of stimulation.

It is interesting to note that over a period of training, the short latency dopamine response shifts from the primary reinforcer to a conditioned stimulus (CS) which predicts the reward[80]. In such circumstances it is likely that the salience of the CS is increased progressively (or habituation prevented) by association with the primary reward (possibly in the amygdala[36]). Consequently, the CS would be expected, increasingly, to interrupt ongoing behaviour throughout training. Thus, in the trained animal, if the CS interrupts ongoing selections and initiates a re-prioritisation favouring actions related to reward acquisition, a further general interrupt when the reward is presented may be unnecessary. It must be emphasised that this suggestion does not preclude dopaminergic transmission from playing an important role in reinforcement. Accumulating data (reviewed by Smith and Bolam[82] and Wickens and Kotter[96]) suggest that dopaminergic input to the striatum could place the system into a state where cortico-striatal synapses are eligible for modification. Thus, in addition to facilitating switching, the early dopamine response could also place the basal ganglia into a 'state of readiness' to modify selections on the basis of subsequent experience.

Multiple switching and functional hierarchies

Additional control problems arise from the existence of multiple output systems which can be

independently regulated (see above). On the one hand, the facility to select simultaneously outputs which co-operate is important, while the concurrent activation of undesirable or incom-patible outputs must be prevented. To solve these problems we suggested above that a hierarchy of selection mechanisms is required (Figure 2). It is possible that the division of the basal ganglia into limbic, associative and motor domains could reflect the presence of such a functional hierarchy. For example, there is evidence that many of the major motivational systems of the brain have connections which converge on the limbic domain of the striatum[2,35,51]. It is possible therefore, that competitions to decide the general course of action could be resolved within limbic domains of the basal ganglia. The winning motivational system (e.g. replenish energy stores) may then selectively prime associated inter-mediate level command systems capable of specifying appropriate patterns of action (food acquisition, consumption, etc.). The selection of actions commanding greatest support could be resolved by competition in associative regions of the basal ganglia. The final choice of specific patterns of muscular activity would then be resolved in the motor domains of the striatum (with candidates primed by selections made at the intermediate level). Note that the interactions between levels is likely to be indirect. An elegant proposal of how the different domains of the striatum might interact has been made be Joel and Weiner[51]. Their suggestion of 'split circuits' in which striatal-cortical interactions are charact-erised as part 'closed-loop' (within domains) and part 'open-loop' (between domains) offers a plausible anatomical substrate for sequential linking of different functional regions of the striatum.

The above discussion suggests that competitions between movements requiring a specific mus-culature are resolved in the motor domains of the striatum. However, most actions involve the simultaneous activation of several groups of muscles. For example, when a rodent turns to bite a target, careful co-ordination of the head and oral control circuitry is required. Anatomical evidence indicates that, in this particular case, resources for controlling the head and mouth may simultaneously be made available by collateralised nigral

outputs[91,99] to the superior colliculus and oral reticular for-mation. This architectural feature suggests that the sensory guidance and co-ordination of head and mouth movements is likely to be conducted in circuitry outside the basal ganglia. Supporting this view are observations, mentioned above[46,72], which show that a rat has no difficulty in co-ordinating the head and mouth movements required to locate and bite an object moving in its whisker field when the basal ganglia output mechanisms are jammed in the 'on' position (although it does lose the ability to habituate this response). In such circumstances co-ordinated reactions required to locate and bite the target must be made in the absence of any sequential inhibitory and/or disinhibitory signals from the basal ganglia. It is possible therefore that selections within the somatotopically organised motor regions of the basal ganglia relate more to the choice of an effector for a particular action (hand, arm, leg, mouth) rather than a specific pattern of muscular activity.

In the future, therefore, it will be important to determine whether the basal ganglia need to organise a simultaneous disinhibition of all parts of the motor plant involved in complex actions, or whether the selection of a particular effector is sufficient. If the latter, it would be assumed that structures outside the basal ganglia co-ordinate activity in different muscle groups to ensure the chosen effector moves appropriately in space[90]. A related issue will be to determine how adaptive processes (possibly located within the basal ganglia[34]) convert successful combinations of individually selected 'unskilled' components of action into the individually selected 'auto-matised' multi-componented sequences which characterise 'skilled' performance.

NEW PERSPECTIVES

In view of the profusion of functions suggested for the basal ganglia we will conclude by considering briefly how this diversity might be reconciled with our proposal for a more 'selective' computational role.

First, the fundamental architecture of the basal ganglia seems to be archaic in evolutionary terms.

The main basal ganglia nuclei appear to have homologues in the brains of all the vertebrate groups, and there is growing evidence that the neurotransmitter organisation and connectivity patterns of the basal ganglia are largely conserved in at least the jawed vertebrates[64], and possibly in all vertebrates[69]. Insofar as structure carries implications for function, this indicates that the basal ganglia might perform a similar role in the nervous systems of all vertebrates. The resolution of competition between systems seeking access to restricted resources (Figure 5) would be a role of sufficient generality. A second reason to expect a relative conservation of function is that the striatum is known to occupy a roughly similar proportion of forebrain volume in all classes[42], whereas both the cerebral cortex and the cerebellum have dramatically increased in size in the evolution of mammals. Perhaps this reflects an increase in the number and sophistication of competing command systems without a corresponding proportional increase in the size of the switch.

An important characteristic of the non-mammalian basal ganglia is that its principle input and output pathways are directed to the midbrain. This suggests that the original role of the basal ganglia may have been to arbitrate between the different demands of multiple midbrain sensorimotor systems. With the expansion of the forebrain in later vertebrates these mechanisms may have been recruited, with little change, to serve a similar role with respect to new, higher-level command systems. If the phylogenetically older basal ganglia circuits are preserved in mammals we might expect that removal of all cortical command systems would leave the selection of midbrain initiated activity intact. A review of the competencies of decorticate rodents suggests this is largely true[92]. The basic forms of ingestion, grooming, sexual behaviour, orienting and defence (specified by brain-stem command systems) survive the removal of most of the rat forebrain. Interestingly, damage to the relevant areas of the basal ganglia seriously compromises the expression of these behaviours[92].

The existence in mammals of a large projection to the basal ganglia from cortical areas that subserve primarily cognitive rather than sensorimotor functions, indicates that the role of the mammalian

basal ganglia may not be confined to the selection of behaviours, actions and movements. Thus, it is possible that the basal ganglia architecture could play a comparable role in cognition to that of action selection in motor control. That is, the basal ganglia may be involved in arbitrating between multiple cortical systems competing for a share of limited memorial or attentional processing[37,48,93]

If the basal ganglia is a specialised device for the solution of selection problems, then a wide variety of brain systems that require access to some limited resource (motor or cognitive), may compete for priority through connections with the basal ganglia. This proposal may begin to explain why the basal ganglia has been implicated in so many diverse functions, and provides a platform from which we can begin to reconsider a host of experimental findings. For example, reviews of the electrophysiological properties of basal ganglia neurones often emphasise the diversity of signals it is possible to record[41,65,79]. However, if as we suggest, the basal ganglia performs selection at many different levels of the functional hierarchy, a wide variety of signal specificities should be expected. Furthermore, insofar as sensory, affective, or cognitive variables contribute to the salience of competing inputs to the striatum, the activity of striatal cells would necessarily reflect corresponding sensory, affective, or cognitive specificities. Consequently, to demonstrate that the firing of a striatal cell correlates with a sensory, affective, or contextual variable is not sufficient reason to conclude that the basal ganglia plays a role in perception, emotion or cognition, other than for the purpose of determining access to limited motor or cognitive resources.

A similar point can be made concerning the interpretation of behavioural literature. There are numerous examples of basal ganglia manipulations either facilitating or disrupting behavioural output[61,75]. Consequently there has been much controversy and debate concerning the effects of such manipulations on motivational, sensorimotor, and motor performance[57]. Acc-ording to the present view, system-wide manipulations which affect all channels would be expected to have general effects on behaviour, such as the akinesia observed following extensive depletions of dopamine[61]. Similarly, manip-ulations restricted to specific regions would be expected to prevent the selection of specific classes of behaviour or movements[52,70]. Again, to show that a particular action is disrupted by a striatal manipulation does not necessarily allow the conclusion that the basal ganglia play an essential role in the planning, initiation, or even the execution of the action, only its capacity to be selected.

Finally, the proposed model provides an interesting perspective on the major basal ganglia disorders in terms of reflecting potential failures of selective function. For example, it is widely acknowledged that one of the important features of Parkinson's disease concerns a general inability to remove inhibitory control from the motor system[65] and difficulties in switching selections[43,47]. Other conditions may be related to failures in mechanisms which suppress activity in non-selected channels, and/or adjust thresholds allowing competitive interrupts (ballism, Huntington's chorea[19], Tourette's syndrome[7], schizophrenia[13]). Finally, in some conditions, there may be disruption to mechanisms which normally terminate a selection by indicating that an action has been successful or that a selection is proving ineffective (obsessive compulsive disorder[67]).

In this commentary, we have looked in the basal ganglia literature for features which can contribute to the solution of a particular computational problem—the requirement for effective and appropriate selection in the vertebrate brain. From this perspective we have shown that many aspects of basal ganglia architecture and function appear to be consistent with the notion of a centralised selection mechanism. In providing this framework we have, necessarily, been selective. Much work is required to see if these 'broad-brush' proposals are consistent with, or are contradicted by, detailed observations reported in the voluminous basal ganglia literature. From a theoretical standpoint there are also many outstanding issues which require further thought. How does the resolution of conflicts at different levels of behavioural analysis allow for the simultaneous selection of non-conflicting actions? What exactly is being selected in different parts of the striatum and how do these 'units of selection' change as the system becomes

skilled/automatised? Of equal sig-nificance will be a thorough consideration of how basic selection processes are modulated, both by current conditions and by experience. It is clear from the complex neurochemistry and feedback circuitry of the basal ganglia[31,33,83] that these adaptive processes are unlikely to be trivial.

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