A State-Space Striatal Model*

Christopher I. Connolly J. Brian Burns

October 28, 1993

1 Introduction

This chapter considers the role of the striatum in computing purposeful state changes. Such state changes include, for example, movement through a maze, or an obstacle-avoiding arm reach. In each of these cases, the system (arm, body, etc.) must make its way from the current state to one or more goal states, avoiding undesirable states along the way. Certain properties of the striatum make it a strong candidate for a locus of computation for this problem.

Alexander et al. [1] present a compelling view of the basal ganglia as being involved in parallel, functionally segregated circuits. These circuits appear to run from cortex, striatum, pallidum, thalamus, and back to cortex (Graybiel 1991 [2]; see also Holsapple, et al. 1991 [3]). Using this basic architecture, this chapter attempts to examine some striatal "cross-sections" of these circuits. We postulate that these cross-sections correspond to distinct, contiguous state spaces embedded in the striatal matrix, each of which is responsible for an aspect of organism function (e.g., arm reaching, egomotion, etc.). We also propose that the membrane potentials of cells in these regions comprise harmonic

*Draft chapter for "Models of Information Processing in the Basal Ganglia", J. Houk, ed., to be published by MIT press.

functions over each state space, and that the gradient descent of these functions produces trajectories – sequences of purposeful state changes.

In (Connolly and Burns 1993a [4]), a striatal model is proposed which suggests that the striatum contains state-space representations. The model concentrates on the motor control aspects of basal ganglia function. This model is reviewed here, and some refinements of the model are considered. In particular:

- The model is further localized to the matrisomes of the striatum. These contiguous partitions of the matrix appear to be in the best position, both anatomically and pharmacologically, for performing the sort of motor control proposed here.
- The effect of continuous cortical firing (of the sort exhibited by pyramidal neurons of layer V) on medium spiny cells is considered.
- A more detailed (albeit speculative) picture is proposed for the communication of gradient (state change) information from the striatum to the pallidum.

The relevant mathematical description of a motor control scheme is reviewed first, followed by a description of the original striatal model. The chapter concludes by considering some extensions and suggested experiments for this model.

2 Motor Control

An important problem in robotics concerns systems which are capable of deriving collision-free paths from one point to another (the path-planning problem). For most robot types, one can describe robot position and motion in terms of the robot's configuration space (Lozano-Pérez 1981, Udupa 1977 citelozano81,udupa77). Configuration space is the space of parameters which can be used to describe the pose of the robot. For a small mobile

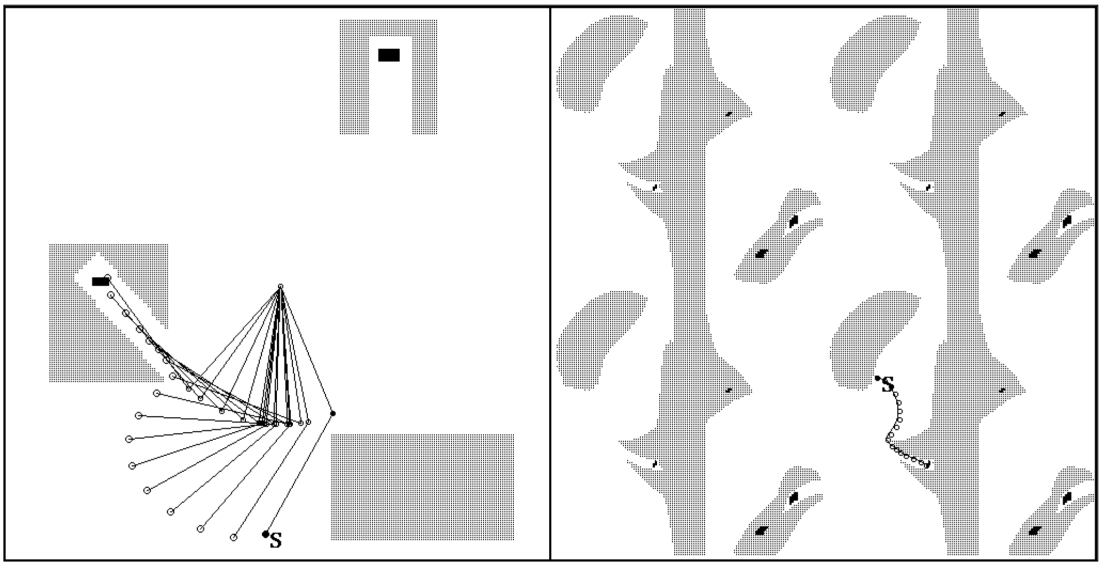


Figure 1: An obstacle-avoiding reach, generated using a harmonic function. Left: 2-link arm avoiding obstacles. Right: Configuration space trajectory.

robot, these parameters are simply the x and y positions of the robot on the floor. For a jointed robot arm, the parameters are the angles of each joint. Thus, such mechanical systems can be represented as single points in an appropriate configuration space. A change in configuration is represented by movement of the point. This scheme has been applied to a variety of mechanical systems.

Figure 1 provides an illustration of these concepts. On the left is a simulation of a 2-link arm with revolute joints. The arm is executing an obstacle-avoiding reach to a goal region. Obstacles are shaded, and the goal region is black. On the right hand side of this figure is the corresponding configuration space, which represents the two joint angles of the robot. Movement of the robot on the right corresponds to the movement of the point on the left. The shaded regions on the right correspond to obstacles.

Although several approaches have been taken for solving the path planning problem in robotics (Schwartz and Sharir 1983; Khatib 1985; Arkin 1989; Canny and Lin 1990 [5, 6, 7, 8]). we concentrate here on the use of harmonic functions (Connolly and Grupen

1992 [9]). Harmonic functions are solutions u to Laplace's equation in n dimensions:

$$\sum_{i=0}^{n} \frac{\partial^2 u}{\partial x_i^2} = 0 \tag{1}$$

This equation describes several physical phenomena (e.g., ideal fluid flow, electrostatic potential) and says that all second derivatives of the harmonic function u sum to zero. The equation provides a model for many steady-state phenomena. The relationship of Laplace's equation to so many different physical phenomena, in concert with its utility for robot planning, makes this mathematical framework a possibility for planning in biological systems.

Analog computers (using resistive networks) have been constructed to compute solutions to this equation, (McCann and Wilts 1949 [10]). Since Kirchhoff's Laws[1] represent a discrete form of Laplace's Equation, such grids are able to compute discrete solutions to Laplace's Equation very rapidly as voltages. Recently, Tarassenko and Blake (Tarassenko and Blake 1991 [11]) employed a resistive grid to solve the path-planning problem for a mobile robot. Simply put, the scheme described here computes potentials governed by Equation 1, then performs gradient descent on the potentials to generate trajectories in some state space.

2.1 State Spaces and Resistive Networks

For the purposes of this discussion, the following intuition may be useful: Consider a robot arm's configuration (joint angle) space. Divide this space into a discrete grid. Every grid point represents a particular arm configuration. Place resistors between pairs of adjacent grid nodes (as shown in Figure 2). This grid can now be used to generate trajectories for

[1]The governing laws for resistances in a circuit: Kirchhoff's current law states that current flowing into a junction must equal the current flowing out of a junction.

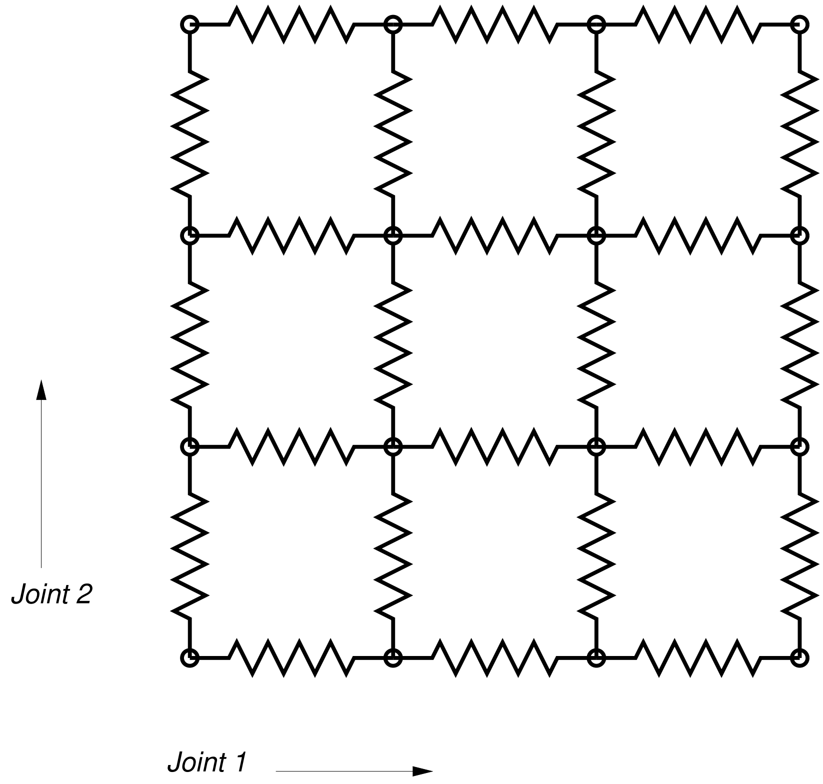
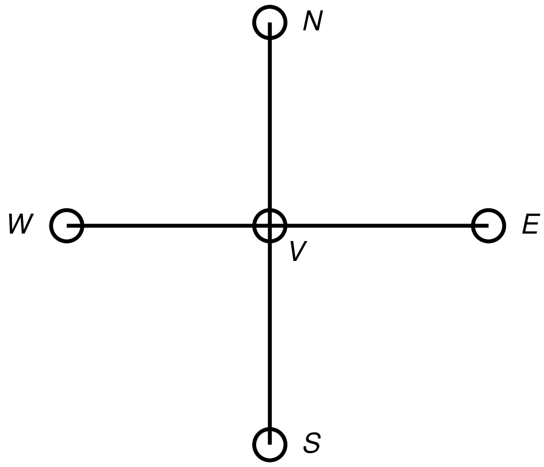


Figure 2: Resistive grid in configuration space.

the robot arm by manipulating voltages at certain nodes. Specifically, the potentials over this grid will be discrete solutions to Equation 1.

In this framework, the setup for motor control is achieved by raising certain grid nodes to high potentials ("depolarization"), and lowering the potentials of other grid nodes ("hyperpolarization"). These potentials then become the boundary conditions for Equation 1. The high potentials correspond to states which are to be avoided (e.g., states which would result in collision with obstacles). Low potentials correspond to goal states. Nodes which are not fixed are referred to as free nodes. To compute the potentials at free nodes, the mean-value property of harmonic functions can be invoked (for example, see Doyle and Snell [12] or Axler et al. [13]): The value of a harmonic function at a point



$$V = \frac{1}{4}(N + E + W + S)$$

Figure 3: Potential at the center is the average of neighbor potentials.

in the grid is the average of the values found at grid neighbors (see Figure 3).[2] This also means that, unless the function is constant in the grid, every free node will be surrounded by nodes with both greater and lesser potentials. This shows directly that such functions are suitable for control based on gradient descent, since the only minima for the function will be at those states which have been held fixed at low potentials. Once such a resistive network has settled, obstacle-avoiding trajectories can be computed by using gradient descent. This basic scheme was used to generate the trajectory seen in Figure 1.

Harmonic functions exhibit properties which are suitable for motor control. In particular, they are smooth, and decrease monotonically toward the designated state-space goal points. The smoothness property results in trajectories which are easily controlled. The monotonicity insures that gradient descent will always reach accessible goal points. A motor control scheme which relies on a resistive network with interpolation[3] (or any

[2]If the conductances ($1/R$) between nodes are allowed to vary, then the center value is the *weighted* average of the neighbors, where the weights are the inter-node conductances. Most of the principles described here will still apply to this case.

[3]Because of the mean-value property for harmonic functions, a simple Gaussian weighted average will

other mechanism for computing harmonic functions) is therefore sufficient for orchestrating smooth, goal-reaching state changes. Moreover, these state changes avoid designated undesirable states. The system to be controlled need only sample the harmonic function gradient at its current state-space point to generate the appropriate trajectory. If the computation method is sufficiently fast, then changes in goal and obstacle configuration will not affect the system's ability to reach its goal safely. Figure 4 illustrates these points. The shaded areas denote obstacles. This figure shows a series of gradient descent trajectories generated by the harmonic function corresponding to the obstacle-goal configuration. Each trajectory terminates at one of four goal points placed close to the obstacles. Note that these paths are all smooth and obstacle-avoiding.

3 Physiological Constraints

The primary neurons of the striatum receive projections from the cortex, and these appear to emanate mainly (but not exclusively) from layer V (Kandel, et al. 1991 [14]). Three general cell types have been identified within the striatum (see Wilson, 1990 [15]):

- Giant Aspiny
- Medium Aspiny
- Medium Spiny

The giant aspiny cells are associated with Kimura's Type I cells (Kimura, et al. 1984 [16]), and are believed to be cholinergic. The medium aspiny cells are believed to be GABAergic. The majority of striatal cells are medium spiny cells, which are also the primary neurons of the striatum. The model presented here focuses on these cells.

provide the required smooth interpolation.

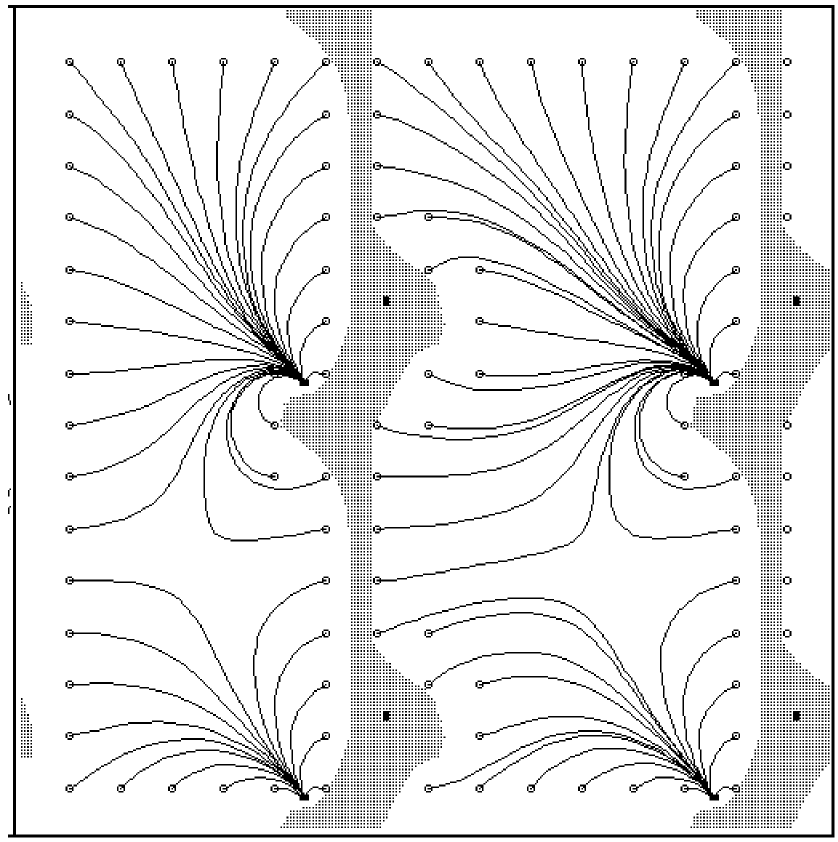


Figure 4: A sequence of trajectories generated by the gradient descent of a harmonic function.

Cortical axons synapse on the spines of medium spiny cells. The medium spiny cells, in turn, project to the globus pallidus and the GABAergic cells of the substantia nigra pars reticulata. The striatal architecture is monosynaptic from cortex to pallidum through the medium spiny cells (Goldman-Rakic and Selemon 1990 [17]). The interneurons (aspiny cells) are much fewer in number and appear to serve a regulatory function. The dendritic fields of the medium aspiny cells are roughly spherical and overlapping. Recent research reports dopamine-dependent dye-coupling among medium spiny cells (Cepeda, et al. 1989;

Walsh, et al. 1989; Cepeda, et al. 1991; Walsh, et al. 1991; O'Donnell and Grace 1993 [18, 19, 20, 21]), and some micrographic evidence which suggests the presence of gap junctions (Pasik et al. 1990 [22]). In addition, the striatum is divided into striosomes (regions which are poor in acetylcholinesterase), and matrix. The matrix is further divided into contiguous matrisomes, which appear to have functional significance (Flaherty and Graybiel 1991 [23]; Flaherty and Graybiel 1993 [24], Graybiel and Kimura, this volume).

Williams and Millar (1990 [25]) report that the activity of medium spiny cells is dependent on dopamine (DA) concentrations. Specifically, DA at low concentrations (roughly 100nM) apparently induces cell firing, while higher DA concentrations (1-10μM) silences the cells. It is conceivable then that, among its other functions, DA can act as a trigger to induce striatal activity.

The Type I cells described by Kimura et al. are tonically active, and become quiescent just before the onsent of voluntary movement. In addition, the striosomes are poor in acetylcholinesterase (AChE), the uptake enzyme for acetylcholine. It therefore seems reasonable to assume that changes in cholinergic cell activity will primarily affect the matrix (see also Graybiel and Kimura, this volume). The matrix also receives a rich set of projections both from motor and sensory areas (Flaherty and Graybiel 1993), and projects in turn to the globus pallidus (Graybiel 1991 [2]).

4 The Picture

In light of the algorithmic scheme described in Section 2.1 and the physiological constraints mentioned in Section 3, an overall view of the striato-pallidal system can be postulated. Figure 5 illustrates those components of the striatum and pallidum which are considered in this discussion.

Cortical neurons which project to the matrix are responsible for imposing constraints on this system. We propose that, at the very least, these neurons set the boundary conditions for striatal computation. The net effect of this activity is that certain striatal primary neurons will be depolarized, while others are hyperpolarized. The network of primary neurons represents a state space (e.g., arm joint angles) over which a potential function (determined by Equation 1) is passively computed, subject to the boundary conditions determined by corticostriatal control. The most direct and rapid possibility for passive computation of a harmonic function is through electrotonic coupling (see Figure 6). This would result in a resistive network within the striatum, probably regulated in part by the (dopaminergic) nigrostriatal system.

The potential function is therefore "sculpted" by the cortically-imposed boundary conditions. One may envision this function as a thin rubber sheet, where some regions have been pulled up (obstacles, undesirable states), while others are pulled down (goal states). If the mechanism for computing this function is fast enough (e.g., a resistive network), then the function need not be completely static, but may change in response to external circumstances (e.g., movement of obstacles). The state change trajectory determined by this surface can be envisioned by imagining the motion of a ball rolling down the rubber sheet.

The gradient of this function must be extracted at the point corresponding to the current state. This provides the system with information about the next immediate state change. In (Connolly and Burns 1993), we postulate that a small region of cells (the current-state cluster) fires to deliver this information to the pallidum. Firing frequency presumably encodes the gradient information. Locally reduced DA concentrations may be responsible for this increased activity (Williams and Millar 1990 [25]). This current-state cluster moves with the change in state, and essentially forms a feedback loop with the cortex providing current state information. In the case of arm movement, for example, the gradient induces a state change (through the pallidum, thalamus, and motor cortex) which changes the arm position. This change in state is manifested as a cortically-induced change in the location of the current-state cluster within the striatum.

5 Refinements and Extensions to the Picture

The medium spiny cells exhibit overlapping dendritic fields and local axonal arborization. Even so, there is currently no evidence for lateral inhibition among the network of medium spiny cells (see Groves, et al., this volume). These cells are relatively quiet, and in concert with this, their subthreshold activity suggests that the sort of passive computation described above could be taking place within the matrisomes. The proposed computation is a relaxation of potentials (Connolly and Burns 1993a [4]). We conjecture that the matrisomes correspond to the "state spaces" described above. These are, at least in a rough sense, striatal cross-sections of the multiple parallel circuits described by Alexander et al. (1992 [1]). This localization is supported by the anatomical connections: afferents from the appropriate cortical sensory and motor areas, and efferents to the globus pallidus. In contrast, the striosomes project mainly to the substantia nigra pars compacta [2]. The involvement of the globus pallidus in motor control (Kato and Kimura 1992 [26]) and its apparent functional segregation (Hoover and Strick 1993 [27]), lend some support to the view of matrisomes as functional units for direct motor control.

Pyramidal neurons of the cortex (some of which appear in layer V) have a regular firing pattern (Douglas and Martin 1990 [28]) which is suitable for maintaining EPSPs (and possibly IPSPs) in a finely graded manner over a period of time in striatal neurons (Wilson 1990 [15]). In addition, striatal medium spiny cells exhibit a pronounced "up" state after coordinated corticostriatal excitation (Wilson, this volume), which could be a manifestation of cortically-imposed boundary conditions.[4] In the context of the model described here, pyramidal neurons could represent a form of short-term state memory. Axonal arborization of corticostriatal fibers allows for a variety of possible mappings from cortical representations to striatal state-space representations. An example of such a mapping is the cartesian to joint space transformation. In hardware, this requires nothing more than a massive boolean "OR" circuit which translates cartesian effector positions into corresponding joint angle "buckets" (Connolly and Burns 1993a). A similar scheme has been used for performing obstacle mappings for robot systems (Connolly and Grupen 1993 [9]). Figure 7 illustrates this mapping. All of the shaded cells in the left grid are mapped (through an "OR" gate) to one cell on the right. A 2-link arm is superimposed on the left. The grid on the right represents joint angles (and thus all whole-arm configurations). In this way, obstacles which are sensed in cartesian coordinates can be mapped directly into a representation in joint space (Figure 1 on the right shows the joint space mapping for a rectangular obstacle). It is possible that this scheme has a counterpart in the cortico-matrisomal projection.

5.1 Gradient Readout

The picture described above still begs the question: How is gradient information transferred from the striatum to the pallidum? Although the striatum is relatively quiet, certain cells do fire in bursts and in response to passive or active arm movement (Crutcher and DeLong 1984 [29], Kimura 1990 [30]). This firing pattern could represent a "readout" of the information inherent in the distribution of membrane potentials in the matrisome network. The current-state cluster of firing cells should be able to transfer the potential gradient information from the current state cluster to the pallidum. To exemplify

[4]It is interesting to note that the "up" state is just *below* the action potential threshold.

this gradient computation, the reduction of DA concentrations is approximated by a spatial Gaussian distribution. Specifically, the increase in cell activity due to reduced DA concentration as a function of cell location is modeled here by:

$$G(x, y, z) = \alpha e^{-\beta(x^2+y^2+z^2)} \tag{2}$$

Here, x, y, and z represent distance from the centroid of the cluster. It is assumed here that the firing rate R of cells within the cluster will depend on the product of DA concentration and membrane potential:

$$R(x, y, z) = G(x, y, z)V(x, y, z)$$

This distribution of firing rates will result in a skewed Gaussian. The position of the peak of this skewed Gaussian is a function of the gradient of V, and thus represents an encoding of the gradient. Figure 8 shows how the slope of a function (top) results in such a skew in the distribution (bottom). The vertical line in the center of the figure shows the location of the peak of the original Gaussian function. In general, only one extremum (a maximum) will occur in this function, since V is harmonic (thus has no extrema in the region of interest) and G is strictly positive with only one maximum. This relationship is determined by differentiating R and finding common zeros (i.e. the extrema of R):

$$\begin{aligned} R_x &= G_x V + G V_x && (3) \\ &= 2\alpha\beta x(x^2 + y^2 + z^2)GV + V_x[DA] && (4) \\ &= G(V_x - 2\alpha\beta x(x^2 + y^2 + z^2)V) && (5) \\ &= 0 && (6) \\ & && (7) \end{aligned}$$

The function G is strictly positive. Thus, at the peak of the skewed Gaussian, the following relationships will hold:

$$V_x = 2\alpha\beta x(x^2 + y^2 + z^2)V \tag{8}$$

$$V_y = 2\alpha\beta y(x^2 + y^2 + z^2)V \tag{9}$$

$$V_z = 2\alpha\beta z(x^2 + y^2 + z^2)V \tag{10}$$

$$\tag{11}$$

Note also that at the origin, the function R_x is proportional through α to V_x (likewise for R_y and V_y, and R_z and V_z), thus implying that most of the mass of R is shifted in the direction of the gradient of V.

This model of striatopallidal firing frequency suggests that the potential gradient is directly related to the centroid of the resulting skewed Gaussian. When the gradient of the potential function is zero, the Gaussian is not skewed. This firing profile sends essentially the same information (a skewed Gaussian through mass/frequency coding) from the striatum to both the internal and external segments of the globus pallidus. Both spines (Wilson 1984 [31]) and intercellular resistances will result in a low-pass filtering for any changes in membrane potential. Because of this, it is unlikely that the action potentials (which are high-frequency signals) within this current-state cluster would have a significant effect on the potentials over the whole matrisomal network.

While this picture is extremely speculative, it is presented in order to give the reader at least one possible picture for the transferral of gradient information from striatal membrane potentials to the globus pallidus.

6 Summary

A striatal model has been outlined here which proposes that the matrisomal networks of the striatum correspond to individual state spaces, each of which govern different aspects of organism behavior. The focus of this description has been on motor control, since this appears to be the most direct way of testing mathematical and algorithmic properties of the model. It is essential to be able to implement mathematical descriptions for striatal motor control in a straightforward manner on artificial mechanical systems (see e.g. Alexander, this volume). This insures a certain *algorithmic* consistency to any proposed scheme.

The choice of matrisomes for the loci of computation is driven by their anatomical and pharmacological properties. These properties appear to be strongly related to a context-dependent motor control function. The similarities between putamen and caudate nucleus, and the existence of other functional units within the caudate nucleus (e.g., Parthasarathy, et al. 1992 [32]) suggest that it should be possible to extend this model to non-motor functions (see, for example Connolly and Burns 1993b [33]).

The model presented here is at best a schematic for one aspect of striatal motor control. In any event, it underscores the algorithmic and biological consistency required for successful models of basal ganglia function. As always, such models are most useful if they can predict new properties of the system being modeled. In the case of this state space model, we can suggest the following as possibilities:

- motor trajectories (e.g., purposful reaches) could be dependent on the presence and permeability of gap junctions.
- membrane potentials of cells within the same matrisome should be related. Specifically, each cell's membrane potential should be a weighted average of neighboring

cell potentials. This suggests that changes in membrane potential for one matrisomal spiny cell should affect the others in the network, to some degree.

- the observed spike duration of matrisomal spiny cells can be estimated and used to predict the intercellular resistances and capacitances which would be required for proper low-pass filtering of action potentials.

- the firing of a cluster of matrisomal cells should produce a stereotyped motor reaction. In the case of an arm, for example, appropriate stimulation should result in a repeatable movement to a particular configuration.

- in Huntington's patients with chorea, repeated and controlled arm movements (e.g., straight-line reaches to a goal point) should reveal "dead" zones, i.e., arm configurations which consistently result in deviations from the appropriate path.

References

[1] Garrett E. Alexander, Mahlon R. DeLong, and Michael D. Crutcher. Do cortical and basal ganglia motor areas use 'motor programs' to control movement? *Behavioral and Brain Sciences*, 15(4), 1992.

[2] Ann M. Graybiel. Basal ganglia – input, neural activity, and relation to the cortex. *Current Opinion in Neurobiology*, 1:644–651, 1991.

[3] James W. Holsapple, James B. Preston, and Peter L. Strick. The origin of thalamic inputs to the "Hand" representation in the primary motor cortex. *Journal of Neuroscience*, 11(9):2644–2654, September 1991.

[4] Christopher I. Connolly and J. Brian Burns. A model for the functioning of the striatum. *Biological Cybernetics*, 68(6):535–544, 1993.

[5] Jacob T. Schwartz and Micha Sharir. On the Piano Movers' Problem I: the case of a two-dimensional rigid polygonal body moving amidst polygonal barriers. *Communications on Pure and Applied Mathematics*, 36:345–398, 1983.

[6] Oussama Khatib. Real-time obstacle avoidance for manipulators and mobile robots. In *Proceedings of the 1985 IEEE International Conference on Robotics and Automation*, pages 500–505. IEEE, March 1985.

[7] Ronald C. Arkin. Motor schema-based mobile robot navigation. *International Journal of Robotics Research*, 8(4):92–112, 1989.

[8] John F. Canny and Ming C. Lin. An opportunistic global path planner. In *Proceedings of the 1990 IEEE International Conference on Robotics and Automation*, pages 1554–1559, May 1990.

[9] Christopher I. Connolly and Roderic A. Grupen. The applications of harmonic functions to robotics. *Journal of Robotic Systems*, 10(7):931–946, October 1993.

[10] G. D. McCann and C. H. Wilts. Application of electric-analog computers to heat-transfer and fluid-flow problems. *Journal of Applied Mechanics*, 16(3):247–258, September 1949.

[11] L. Tarassenko and A. Blake. Analogue computation of collision-free paths. In *Proceedings of the 1991 IEEE International Conference on Robotics and Automation*, pages 540–545. IEEE, April 1991.

[12] Peter Doyle and J. Laurie Snell. *Random Walks and Electric Networks*. Carus Monographs in Mathematics. American Mathematical Society, 1984.

[13] Sheldon Axler, Paul Bourdon, and Wade Ramey. *Harmonic Function Theory*, volume 137 of *Graduate Texts in Mathematics*. Springer-Verlag, New York, 1991.

[14] Eric R. Kandel, James H. Schwartz, and Thomas M. Jessell, editors. *Principles of Neural Science*. Elsevier Science Publishing Co., 1991.

[15] Charles J. Wilson. Basal ganglia. In Gordon M. Shepherd, editor, *The Synaptic Organization of the Brain*, chapter 9. Oxford University Press, New York, 1990.

[16] Minoru Kimura, Janusz Rajkowski, and Edward Evarts. Tonically discharging putamen neurons exhibit set-dependent responses. *Proceedings of the National Academy of Sciences, USA*, 81:4998–5001, August 1984.

[17] P. S. Goldman-Rakic and L. D. Selemon. New frontiers in basal ganglia research. *Trends in Neurosciences*, 13(7):241–244, 1990.

[18] Carlos Cepeda, John P. Walsh, Chester D. Hull, Sherrel G. Howard, Nathaniel A. Buchwald, and Michael S. Levine. Dye-coupling in the neostriatum of the rat: I. modulation by dopamine-depleting lesions. *Synapse*, 4:229–237, 1989.

[19] John P. Walsh, Carlos Cepeda, Chester D. Hull, Robin S. Fisher, Michael S. Levine, and Nathaniel A. Buchwald. Dye-coupling in the neostriatum of the rat: II. decreased coupling between neurons during development. *Synapse*, 4:238–247, 1989.

[20] Carlos Cepeda, John P. Walsh, Nathaniel A. Buchwald, and Michael S. Levine. Neurophysiological maturation of cat caudate neurons: Evidence from in vitro studies. *Synapse*, 7:278–290, 1991.

[21] Patricio O'Donnell and Anthony A. Grace. Physiological and morphological properties of accumbens core and shell neurons recorded in vitro. *Synapse*, 13:135–160, 1993.

[22] Pedro Pasik, Tauba Pasik, and Gay R. Holstein. The ultrastructural chemoanatomy of the basal ganglia: 1984-1989 I. The neostriatum. In G. Bernardi, editor, *The Basal Ganglia III*. Plenum Press, New York, 1990.

[23] Alice W. Flaherty and Ann M. Graybiel. Corticostriatal transformations in the primate somatosensory system. projections from physiologically mapped body-part representations. *Journal of Neurophysiology*, 66(4):1249–1263, 1991.

[24] Alice W. Flaherty and Ann M. Graybiel. Two input systems for body representations in the primate striatal matrix: Experimental evidence in the squirrel monkey. *Journal of Neuroscience*, 13(3):1120–1137, 1993.

[25] G. V. Williams and J. Millar. Concentration-dependent actions of stimulated dopamine release on neuronal activity in rat striatum. *Neuroscience*, 39(1):1–16, 1990.

[26] Makoto Kato and Minoru Kimura. Effects of reversible blockade of basal ganglia on a voluntary arm movement. *Journal of Neurophysiology*, 68(5):1516–1534, November 1992.

[27] John E. Hoover and Peter L. Strick. Multiple output channels in the basal ganglia. *Science*, 259:819–821, February 1993.

[28] Rodney J. Douglas and Kevan A. C. Martin. Neocortex. In Gordon M. Shepherd, editor, *The Synaptic Organization of the Brain*, chapter 12. Oxford University Press, New York, 1990.

[29] M. D. Crutcher and M. R. DeLong. Single cell studies of the primate putamen II. relations to direction of movement and pattern of muscular activity. *Experimental Brain Research*, 53:244–258, 1984b.

[30] Minoru Kimura. Behaviorally contingent property of movement-related activity of the primate putamen. *Journal of Neurophysiology*, 63(6):1277–1296, June 1990.

[31] Charles J. Wilson. Passive cable properties of dendritic spines and spiny neurons. *Journal of Neuroscience*, 4(1):281–297, January 1984.

[32] H. B. Parthasarathy, J. D. Schall, and A. M. Graybiel. Distributed but convergent ordering of corticostriatal projections: Analysis of the frontal eye field and the supplementary eye field in the macaque monkey. *Journal of Neuroscience*, 12(11):4468–4488, November 1992.

[33] Christopher I. Connolly and J. Brian Burns. A new striatal model and its relationship to basal ganglia diseases. *Neuroscience Research*, 16:271–274, 1993.

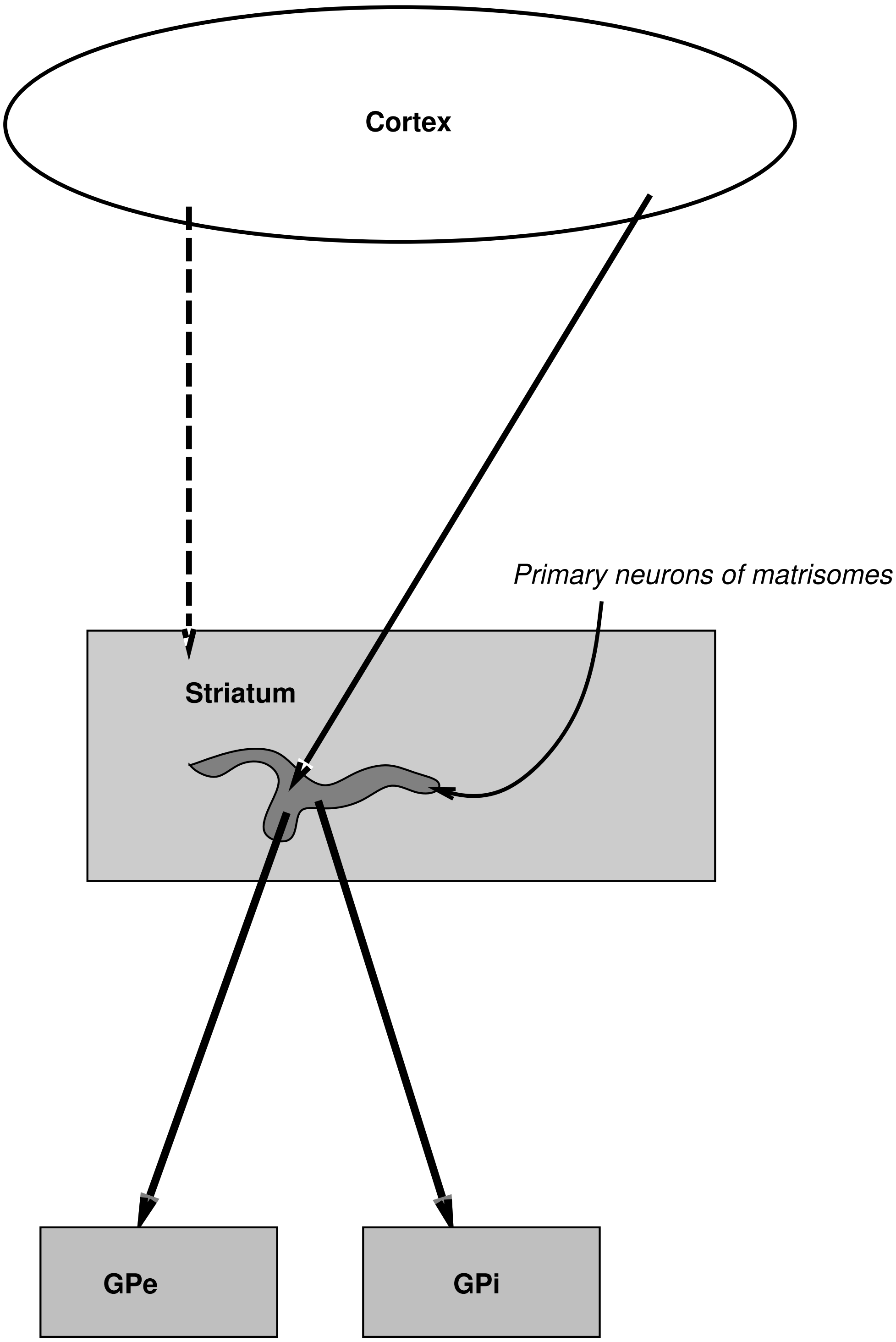


Figure 5: Schematic view of the system under consideration: the cortico-striato-pallidal pathway through the matrisomes.

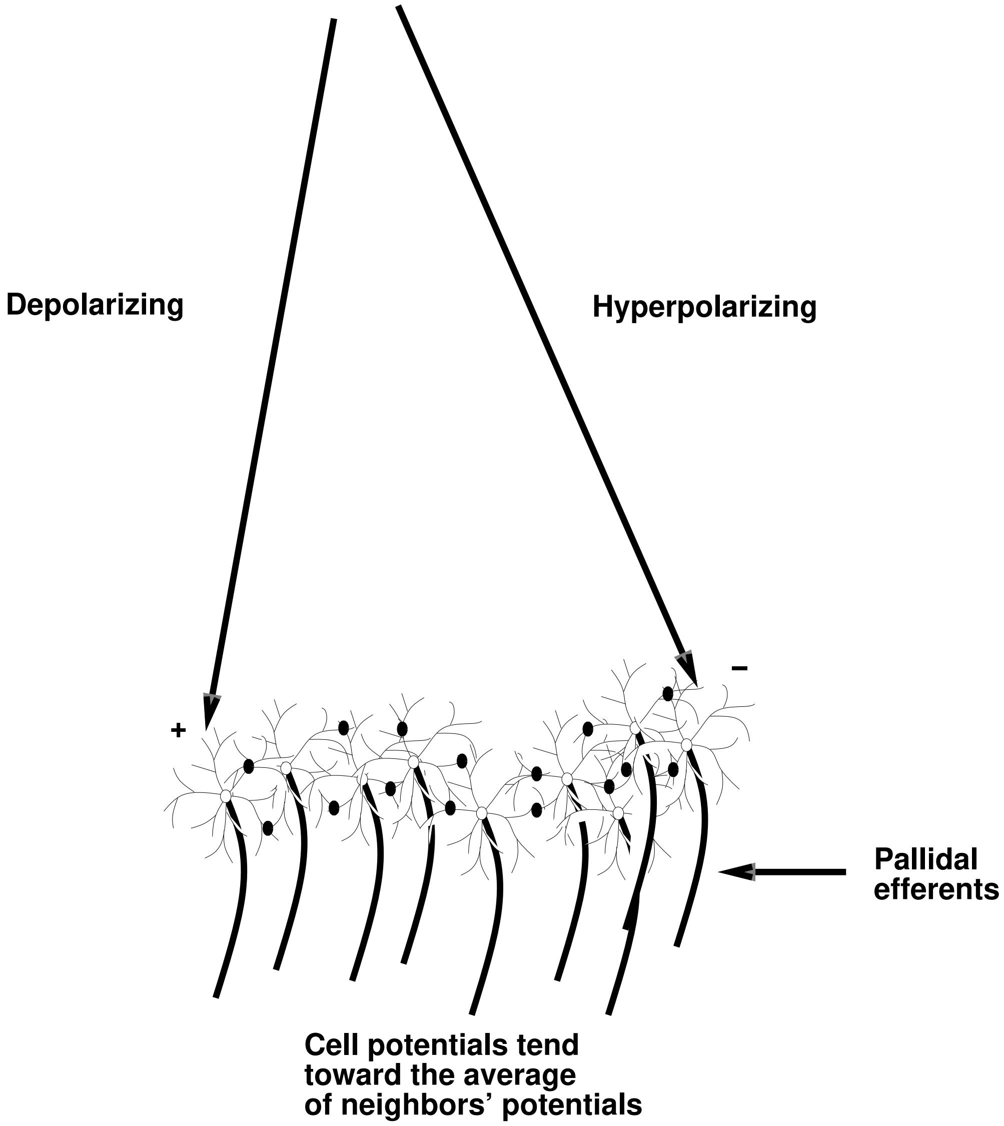


Figure 6: Coupled primary neurons: "free" cells' potentials will be the average of neighbor cells' potentials. Cells marked "+" and "-" are held at fixed potentials.

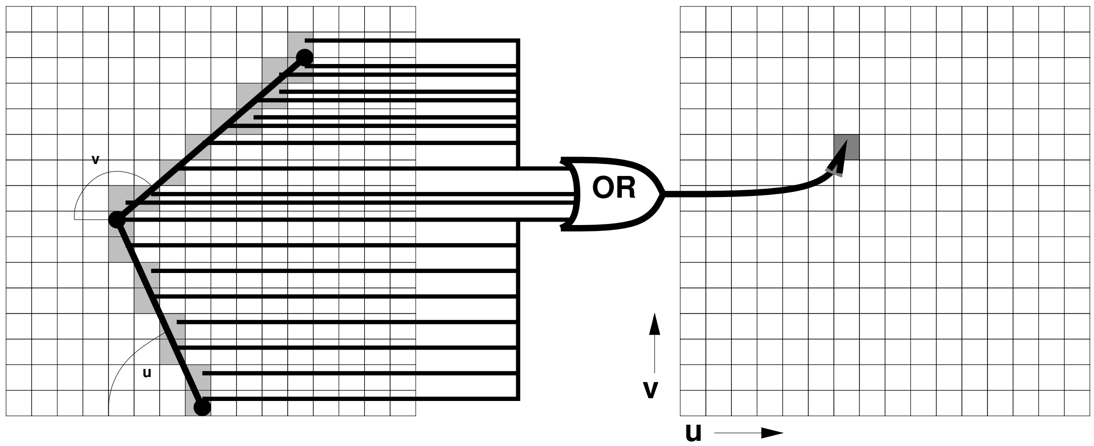


Figure 7: An example of a boolean "OR" circuit which transforms cartesian obstacle information into joint angle space.

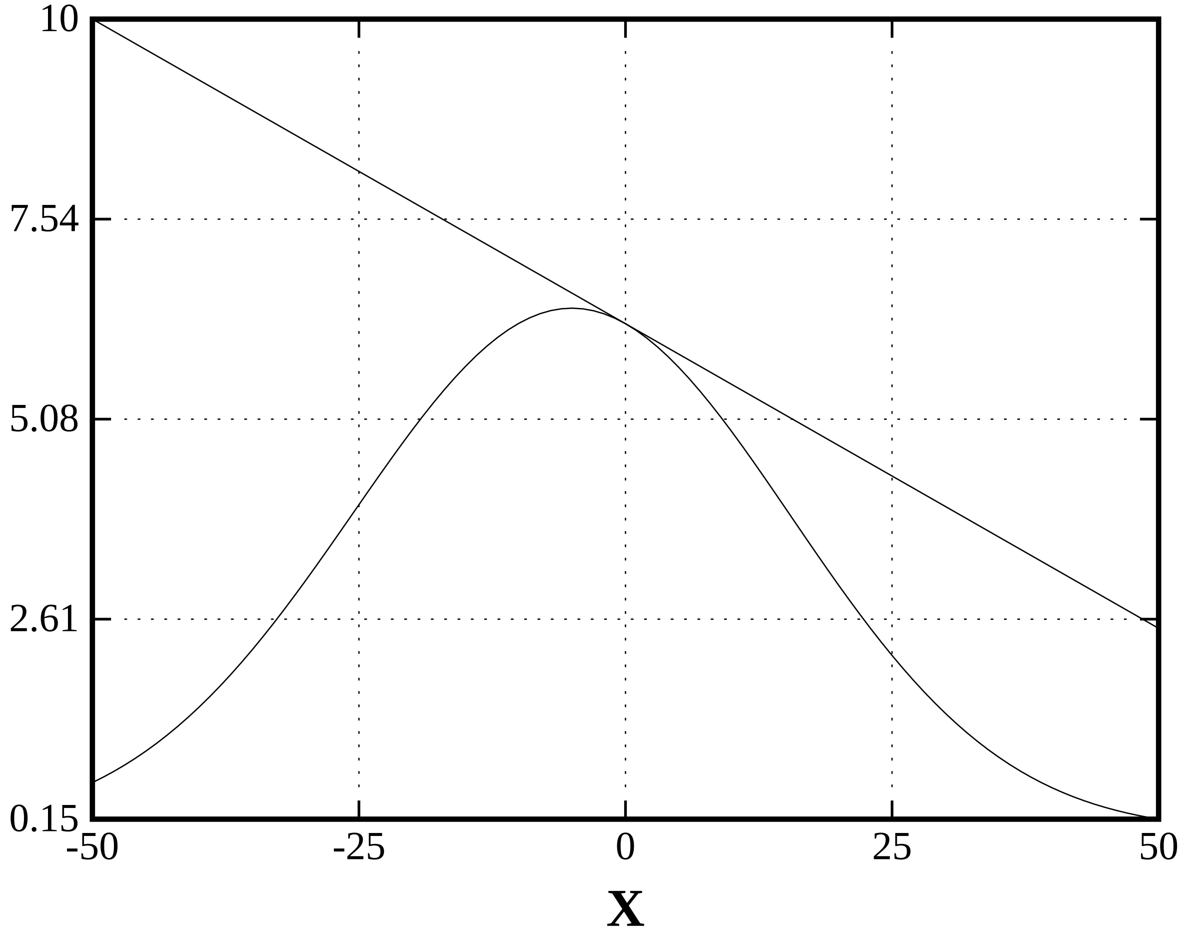


Figure 8: Function R (lower curve) which is the skewed Gaussian resulting from the slope seen in the top curve. Note that the leftward shift in the peak is in the direction of the gradient.