The Planning of Actions in the Basal Ganglia*

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In this abstract, a new theory is put forth on the mechanisms of the planning of goal-oriented and obstacle-avoiding behavior in biological systems. It is argued here that the basal ganglia may be an important locus for aspects of these activities. Furthermore, the mechanisms for its function may in part be characterized as the computation and storage of harmonic functions in parameter spaces associated with the positions and movements of various body parts, and possibly additional representations of action and intention. This abstract is intended primarily to offer a theory for aspects of biological motor planning, which has been motivated by recent research in robotics. An expanded discussion of the material found here, with citations, can be found in Connolly and Burns [1].

Several approaches have been taken for solving the robot path planning problem (see Connolly and Grupen [2] for references). Recent work in robot path planning by Connolly, et al. revolves around the use of harmonic functions for complete robot path planning. Harmonic functions are solutions to Laplace's Equation. This equation describes several physical phenomena, one of which was exploited by Tarassenko and Blake [3] for a hardware implementation of harmonic function planning. This consists of an array of transistors which are used as a programmable resistive grid. Since Kirchhoff's Law is a discrete form of Laplace's Equation, such a grid is able to compute harmonic functions very rapidly. This grid may have a biological analogue.

The model presented here is primarily concerned with two nuclei of the basal ganglia: the putamen and to a lesser extent, the caudate nucleus (collectively termed the neostriatum). The putamen receives projections specifically from the primary motor cortex, the supplementary motor area, the premotor cortex, and the somatosensory cortex [4]. In particular, premotor cortex ablations are known to affect obstacle avoidance in reaching behavior. The origin of the cortico-striatal projections is consistent with experiments showing the involvement of the putamen in motor function. Moreover, these projections are somatotopic, and divide the putamen into contiguous regions corresponding (in primates) to the arms, legs, face, and hands.

Several researchers have reported that subjects with damaged basal ganglia have significant deficits in the ablity to localize and orient themselves with respect to environmental stimuli or maps representing the environment. Patients with Parkinson's disease, an affliction strongly associated with the basal ganglia, have difficulty using maps to walk through a course. Rats with lesions in the basal ganglia perform poorly in maze traversal. In general, the nature of basal ganglia input and output, and the cellular response timing during sensorimotor tasks seems appropriate for a planning role, as well as other aspects of motor control.

Our model suggests that the basal ganglia are an integral part of the brain's planning machinery. We do not wish to suggest that planning is the *exclusive* domain of the basal ganglia, only that the basal ganglia can perform many planning functions. In contrast to models which suggest selection of a motor program, we propose that the basal ganglia actually create (or plan) the program by performing a gradient descent on a harmonic function, in effect generating a trajectory which describes the successive state changes needed to reach the desired state. The harmonic function is produced by a relaxation process on the membrane potentials within cells in the neostriatum. This relaxation process results from two factors: a) cortically "programmed" high and low membrane potentials at different regions within the neostriatum and b) electrical coupling of the cells via gap junctions.

1 Biological Background

The cells in the neostriatum have been divided into three groups [5]: giant aspiny, medium aspiny, and medium spiny. Although the aspiny cells play an important role, they do not form the main input-output

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path through the striatum. Their function appears to be regulatory in nature. Medium spiny cells are the primary cells of the neostriatum and comprise 70-90% of that tissue in mammals. They receive direct excitatory cortical input, and are the primary output neurons for the neostriatum. Several researchers have shown clearly that medium spiny neurons fire in direct relation to passive and active joint movement.

The neurotransmitter glutamate is supplied by the cortex, and medium spiny cells produce the neurotransmitter GABA. The neurotransmitter dopamine is supplied to the neostriatum by another body, the substantia nigra. Heinonen et al. have shown that glutamate elevates membrane potentials in medium spiny cells. Glutamate typically drives membrane potentials toward 0 mV. Glutamate can also induce the release of GABA in medium spiny cells. Recent studies support the notion that GABA can serve to "clamp" medium spiny membrane potentials at the -50 mV level. Williams and Millar show that dopamine at low concentrations apparently induces cell firing, while higher dopamine concentrations prevents firing.

Dye-coupling experiments suggest that gap junction coupling may exist between medium spiny cells. Gap junctions allow a cytoplasmic, hence electrical connection between cells. It is known that dopamine modulates such coupling within the visual system and cardial cells. Recent dye-coupling experiments suggest that this is also true in the neostriatum. If electrotonic communication is occurring among the medium spiny cells of the neostriatum, then these cells are effectively behaving as programmable resistors.

2 The Model

We propose that medium spiny neurons effectively form a resistive network which is programmable via cortical input. Somatotopic projections exist from the cortex into contiguous, non-overlapping regions within the putamen. This suggests that the putamen can be divided into functional units corresponding to the limbs and face. We propose that each of these units is map of the state space (e.g., joint space) of the corresponding limb. Cortical input sets up the potential function by directly depolarizing certain medium spiny cells using glutamate, and indirectly clamping other medium spiny cells via dendritically-released GABA. The difference in potentials thus produced is propagated among the remainder of neostriatal medium spiny neurons, whose membrane potentials are left to relax to the mean values.

We propose that resistive coupling is responsible for actually computing the potential function. The membrane potential of each medium spiny cell corresponds to the function value. Higher (glutamate-induced) potentials could represent repelling states, while low (GABA-induced) potentials indicate goal states. It has also been shown that the spines on medium spiny neurons act as a low-pass filter (Wilson, in [5]). This greatly diminishes the effect of an action potential on membrane potentials at the dendrites. Such a filtering effect would serve to protect the integrity of the potential function being computed. Local, high-frequency, temporary changes to a cell's potential would therefore have a minimal effect on the potential function. Such a system would result in very few neurons actually firing at any given time, since the vast majority of neurons would be computing the function passively via gap-junctions (and indeed, medium spiny cells are normally rather quiet).

Once computed, the function can be used to drive state changes within the organism. We propose that at any one time during the execution of movement, only a small cluster of medium spiny cells will fire within the neostriatum. We postulate that dopamine is acting as a thresholding mechanism to induce these selected cells to fire. One can make an analogy of this cluster to a ball rolling down the potential surface. The cluster of firing cells changes as movement progresses, but tends to migrate in a continuous fashion toward those cells which represent the organism's goal state. Once the organism has reached the desired state, the process terminates.

References

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