A model of short and long range selective processing in neostriatum

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Introduction

The neostriatum is a major component of the basal ganglia, a set of sub-cortical structures which is critical in shaping movement and cognition. Within the dorsal division of the basal ganglia, the neostriatum is the main input nucleus and, in the rat, constitutes approximately 95% of the neural cell count in the division as a whole. An understanding of neostriatal function is, therefore, crucial for an understanding of the dorsal basal ganglia and, in seeking this function, it is reasonable to suppose that it must be consonant with the operation of the basal ganglia *in toto*. Several functions have been ascribed to the basal ganglia but one recurring theme in the literature is that they are associated with some kind of selective processing. Our recent work has developed the idea of selection, in the context of choosing between behavioural actions, as a unifying hypothesis of basal ganglia operation (Redgrave et al., 1999, Gurney et al., 2001a, Gurney et al., 2001b).

The possibility that neostriatum implements a selective function is a widespread notion, although computational models have hitherto emphasised the importance of competition between members of the dominant cell population of medium spiny projection (MSP) neurons (e.g Wickens 1993, Kotter and Wickens 1995). Such competition requires functional GABAergic connections between these cells, a feature which has, until recently, been called into question. However, several labs have now reported such functionality, thereby reinvigorating the construction of models incorporating it.

The neostriatum also contains three populations of interneurons comprising only 5% of the total cell count. One of these, the fast spiking GABAergic (FSG) interneurons have the capability of mediating short timescale selection dynamics (the other two classes appear to be implicated in longer term modulatory processes). These neurons receive significant cortical input and make contact with MSP neurons at synapses with fast acting $GABA_A$ receptors. The inhibitory nature of FSG interneurons makes them good candidates for mediating a selective function and their connectivity suggests that this might operate over a larger spatial scale than that of MSP neurons. Thus, FSG interneurons are interconnected via electrical gap junctions (Kita et al., 1990) thereby enabling them to integrate cortical activity in a continuous synctitium over a much wider range than MSP neurons. Further, FSG interneurons have larger projective fields than MSP neurons. We therefore sought to examine the possible role that FSG interneurons might play in mediating a long range selective function in neostriatum, and how this might interact with short range processes making use of MSP neurons.

Method

Our model consisted of a network using model neurons obeying leaky-integrator dynamics with a continuous (firing rate) output, and whose afferent driving force was formed by the weighted sum of its inputs. There were 8100 MSP 'neurons' arranged on a square grid, each one making inhibitory contact with its neighbours in a square region with 12 neurons on a side. Each model MSP neuron received a single effective cortical input. The FSG 'interneurons' were sparsely but regularly placed on the same grid. Each interneuron integrated its 'cortical' input across a square neighbourhood of width 18 (representing widespread connectivity via gap junctions) and innervated a group of projection neurons in a region 32 cells wide. Two main classes of input were used. First, those consisting of focussed activity in a few selected locations on the net, spatially separated to fall both within, and outside, the local interconnectivity domain of MSP neurons, but within the receptive field of the FSG interneurons. Selection was deemed to occur between two active sites if the output on one site was suppressed to zero while that of the other remained high. A second class of input consisted of activity at many, randomly chosen locations in order to examine dependence of selectivity on overall input levels.

Results

- Separate short and long range processes mediated by the MSP neuron and FSG interneuron nets could be identified; each network could be separately disabled while retaining selection at the spatial scale of the other.

- Ratios of FSG to MSP neurons that are roughly the same as those supposed to prevail in neostriatum (1:50) worked well. Massively increasing FSG interneuron numbers resulted in the requirement of having to reduce the FSG-to-MSP neuron weight to extremely small values in order to obtain selection and, under these circumstances, there was much reduced contrast in MSP neuron output signals (reduced output level of 'winning' nodes).

- The selectivity was quite sensitive to the FSG-to-MSP neuron weight in the context of the overall level of input. While this is of itself not necessarily a desirable property, there is a putative mechanism in basal ganglia that could provide an adaptive response to input of the right kind. Thus, globus pallidus provides inhibitory projections to striatum which selectively innervate FSG interneurons (Bevan et al 1998). Arguments based on predictions form our system level models of basal ganglia suggest that pallidal control will work in the right direction to supply increased inhibition of the FSG interneuron network as cortical input increases.

- Long range selection was promoted in parameter regimes that enforced large activity levels in the FSG interneurons. This is consistent with the observation that these neurons display burst activity with large spike rates (hence their name) when active.

Conclusion

A network model of neostriatum based on the known micro-circuitry of two of its cell populations is able to mediate both long and short range selective processes. Restructuring the

network in non-biologically plausible ways resulted in a deterioration in selectivity, supporting our selection hypothesis. Cell activity levels are consonant with that observed *in vivo*, and we are able to suggest a possible role for a basal ganglia pathway whose function has hitherto remained obscure.

References

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