THE BASAL GANGLIA: "MINIMAL COHERENCE DETECTION" IN CORTICAL ACTIVITY DISTRIBUTIONS

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INTRODUCTION

The basal ganglia are strongly involved in specific, motivation- and reward-mediated aspects of cortical processing: perception, cognition and action (Hikosaka et al., 1989). These aspects particularly concern "changes" in cortical activity modes (Mink and Thach, 1991), to which the basal ganglia contribute by "gating" of cortical and premotor activity via disinhibition (Chevalier and Deniau, 1990). The interactions between cortex and basal ganglia seem to be organized in multiple parallel loops (Alexander et al., 1986), with lateral competition between these loops as a possible mechanism for cortical cell assembly selection (Wickens et al., 1991).

The concept of "parallel processing" however, is problematic in view of the highly divergent-convergent projections from the first level of the basal ganglia circuit - the neostriatum - to its output nuclei, both anatomically (Percheron et al., 1984) and functionally (Tremblay and Filion, 1989). Given these strongly integrative properties of the basal ganglia, both within and between loops, it is not clear how the basal ganglia could contribute in any specific way to cortical function.

Any theory on basal ganglia function has to be adequately connected to a theory of cortical coding and function. Thus, we will ask, which solution the basal ganglia can provide to the problem of sequential cell assembly activation (Hebb's "phase sequences", 1949). In particular, we will present a theoretical framework which explains the local operations that are performed in the neostriatum, and why these are followed by a sequence of nuclei with strong integrations in the intervening projections.

We propose that the basal ganglia are optimally suited, both anatomically and functionally, to perform a "minimal coherence" analysis of changes in the cortical activity distribution in order to organize reward-mediated sequential behaviour. This evaluation of "coherence" is performed in a similar way the visual system evaluates the optical flow field in order to separate "figure" from "ground". We will develop this idea for the particular case of the motor loop (Alexander et al., 1986), but we emphasize this to be the general principle according to which the basal ganglia contribute to any kind of cortical processing.

The Basal Ganglia IV, Edited by
G. Percheron *et al.*, Plenum Press, New York, 1994

CELL ASSEMBLIES AS THE BASIC SUBSTRATE FOR CORTICAL CODING AND FUNCTION

The cortex can be viewed as a memory structure with a large number of similar elements, showing a high degree of convergence/divergence in their input/output connectivity (Braitenberg and Schüz, 1992). In particular the connectivity patterns of cortical pyramidal cells involve many different cortical areas (Selemon and Goldman-Rakic, 1988) and are assumed to be modifiable by local learning rules. In such types of neural networks, information theory favours the principle of "sparse coding" (Palm, 1982), stating that a functional group of only a very limited number of elements is activated in unison in the coding, storage and recall of a feature or constellation of features. One way how the activation of such an identifiable group can be envisaged is by synchronization: a group of neurons is temporarily separated from the entire neuronal population, when their spike activities become synchronized over some period of time. Such a group of neurons makes up a cell assembly (Gerstein et al., 1989; Erb and Aertsen, 1992; Neven and Aertsen, 1992). Recent experimental studies in the visual cortex suggest that such synchronized activity in groups of neurons may serve perceptual integration by means of feature linking (for a review see Engel et al., 1991).

The mechanism for generating such synchrony - which is not necessarily time-locked to an external stimulus or behavioral event - might at first sight be thought to reside in strong anatomical connectivity. Several arguments, however, speak against this scheme. First, strong anatomic coupling is not a flexible means to organize cells into groups and would, in fact, lead to dedicated groups of neurons, very much like a "grandmother assembly". Moreover, experimental evaluations of multiple-neuron recordings have revealed that strong synaptic coupling is, in fact, quite rare in the cortex (e.g. Abeles, 1982, 1991). Instead, the "effective connectivity" (Aertsen et al., 1989, 1991) between cortical neurons turns out to be generally weak, and highly dependent on stimulus and behavioral context. Moreover, it is remarkably variable over time, with time constants of modulation as low as tens of milliseconds (for a review see Vaadia and Aertsen, 1992). Such context-dependent, rapid modifications of effective coupling - sometimes referred to as dynamic linking - were established in several different cortical areas (e.g. Aertsen and Gerstein, 1991; Vaadia et al., 1991). Theoretical considerations based on these findings have suggested an alternative and much more flexible scheme for generating synchrony. It was shown that the influence of a presynaptic neuron onto the spike activity of its postsynaptic target neuron (i.e. their effective coupling) is critically dependent on the population background activity and only partially reflects the underlying anatomical connectivity (Aertsen and Preissl, 1991). Thus, rapid modulations of coupling can be induced by "dynamic convergence" of activity from the entire network onto the observed neurons, in particular by temporal variations of the rates (Boven and Aertsen, 1989) and the internal coherence (Bedenbaugh et al., 1988, 1990) of background firing (see also Bernander et al., 1991).

The picture which emerges from these considerations on neuronal assemblies is a highly dynamic one: the formation of synchrony is based on rapidly changing synaptic couplings. Thus, a pyramidal neuron is able to rapidly change allegiance and thereby take part in various different cell assemblies, either switching from one to the other or joining a number of them simultaneously, depending on the immediate computational demands.

CHANGE OF CORTICAL ACTIVITY DISTRIBUTIONS: CODING OF TRANSITIONAL PROBABILITIES

A cell assembly may code for a certain stimulus feature or motor program, and can be active in various behavioural contexts (Vaadia and Aertsen, 1992). At the next higher level of organization, a "set" of cell assemblies is conceived to code for a certain constellation of features and/or actions in some behavioural context; activation of such a set constitutes the cortical activity distribution. Clearly, such a set of cell assemblies should not be considered as a cell assembly itself: otherwise one would lose combinatory power to represent different contexts having common features (von der Malsburg, 1986).

A related problem arises when considering the ordered activation of (sets of) cell assemblies in time. According to the theory on cortical "synfire chains" (Abeles, 1982,

1991), once a cell assembly is activated it is able - given the appropriate cross-connectivity - to activate a new assembly. Thus, "synfire chains" or "reverberating synfire chains" (Abeles et al., 1993) seem to be a promising new approach to organize a highly ordered time structure in cell assembly activation (Bienenstock, 1991). One important aspect of time structured activity, however, is missing so far. Consider, for instance, a change in an animal's environment. The animal will respond to this change with a certain motor behaviour, which itself is governed by sequential activation of a certain set of cell assemblies. How can we imagine that the composition of this set and/or its activation sequence is modified by the outcome of the behaviour? The answer is "reward-mediated learning", leading to the formation of a new scheme for cell assembly activation which is more appropriate under the new circumstances (Miller et al., 1990). Note that this reward-mediated plasticity, modifying the transitional probabilities between (sets of) cell assemblies, should be distinguished from the plasticity involved in the establishment of the cell assemblies themselves; the two operate at different levels of organization.

In summary, the problem of organizing sequentially ordered cell assembly activation turns out to be related to the task of tuning the transitional probabilities between (sets of) cell assemblies, guided by experience via a reward signal. We propose the basal ganglia constitute a very elegant implementation of this task.

THE CORTICO-STRIATAL PROJECTION: THE STRIATUM AS A "RETINA" FOR CORTICAL TOPOLOGY

In this part we will show that the particular features of the cortico-striatal projection provide a simple strategy in order to map cortical cell assembly dynamics. Cortico-striatal projection cells are densely scattered throughout cortical layer III and upper layer V (Goldman-Rakic and Selemon, 1984). Hence, it is reasonable to assume that the cortico-striatal projection can transmit detailed information about the entire cortical activity distribution to the striatum.

Moreover, this projection is highly divergent. Local dye injections into the cortex revealed widely distributed "patchy" axonal termination areas in the neostriatum (see Percheron et al., 1984; Goldman-Rakic and Selemon, 1984; Flaherty and Graybiel, 1991; Parthasarathy et al., 1992). However, already at this level of the basal ganglia loop there is also strong convergence. If we think of multiple cortical areas projecting in multiple patches to the neostriatum, there will be considerable overlap within the neostriatal volume occupied by the dendrites of a medium-sized spiny projection neuron (principal cell).

This topographical overlap on the neo-striatum "surface" partly preserves functional neighbourhood in cortical topology, even across different cortical areas. This is demonstrated by detailed mappings of projections from well defined cortical areas: in the caudate nucleus, for example, projection fields from the supplementary and the frontal eye fields closely overlap with one another (Parthasarathy et al., 1992). This overlap, however, is not complete: the two functionally related cortical areas have a "core" where their projection areas onto the neostriatum overlap, but this is surrounded by "shells" with no overlap. We will see that this arrangement is essential to allow the organization of new combinations of cortical cell assemblies.

Let us consider the consequences of these particular features of the cortico-striatal projections in a simple example. We assume three cortical pyramidal neurons *a*, *b* and *c*, each one in a different cortical area *A*, *B* and *C*. The neurons project to a certain striatal area (Fig. 1, λ) having multiple termination fields. Each of the neurons takes part in cortical cell assembly formation. We start with neurons *a* and *b* taking part in one cell assembly. Thus, their discharge will be synchronized for a brief period of time. Since neurons within an assembly are functionally related, their termination fields are likely to overlap. Striatal principal neurons in the regions of overlap receive synchronized excitatory input and, hence, are likely to discharge (Fig. 1) and to establish intersection domains with "winner dynamics" in the local lateral inhibition network (Wickens et al., 1991). A prominent feature of such lateral inhibition networks is the phenomenon of spatial disinhibition. Thus, the intersection domains with "winner dynamics" will support the excitation of principal cells, located at a certain mean disinhibitory distance outside these intersection domains. We have indicated one such "new" domain with disinhibition-induced activity in Figure 1

(asterisk). Let us consider now three possible changes of the temporal association of these cortical neurons, and their consequences for the activity dynamics in the striatum:

1. Neuron *b* switches in synchronization from neuron *a* to neuron *c*. This change of "cortical" liaison leads to a stabilization of the new striatal intersection domain *bc* (Fig. 1, asterisk) and a decrease in activity of the former intersection domains *ab*.

2. Neuron *a* switches in synchronization from neuron *b* to neuron *c*. This cortical change leads to a destabilization of the previously favoured striatal intersection domains *ab* and, in addition, will establish the new intersection domain *ac* (Fig. 1, dotted area).

3. Neuron *c* becomes synchronized with both neurons *a and b*. At first sight this would seem to lead (as in the first case) to a stabilization of the new intersection domain *bc*, however, without weakening the original ones (*ab*). In addition, however, yet another new intersection domain will form (*ac*, dotted area), which will engage in a competition with the previous intersection domains *ab*. This, in turn, will also weaken the intersection domain *bc*, due to a reduction of the spatial disinhibition. Consequently, this last change in cortical association leads to a complete re-adjustment of the spatio-temporal activity pattern in the striatum.

Thus, we conclude that the patchiness of the cortico-striatal projection can be viewed as a strategy to map the dynamic linking of neurons in the cortex to a unique change in spatio-temporal activity patterns in the striatum.

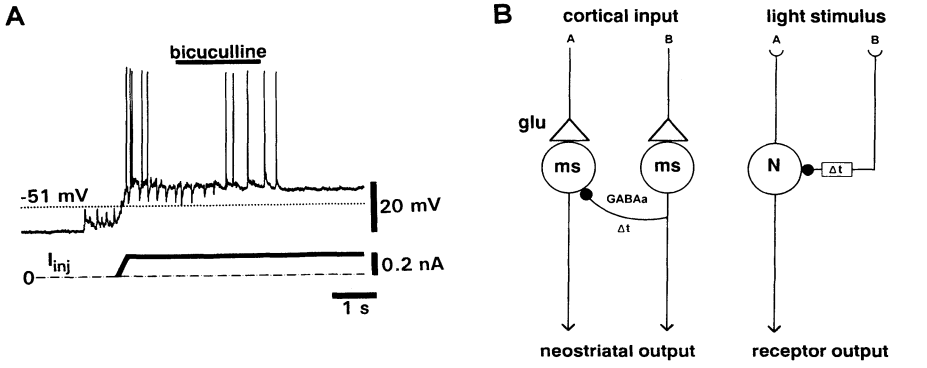

Figure 1. Dynamic linking of cortical neurons is accompanied by a change in the striatal activity patterns. Three cortico-striatal projection neurons have multiple projection fields in the striatum. The spatio-temporal activity pattern in the striatum critically depends on the dynamic linking among the temporal association of these cortical neurons (for further details see text).

THE LATERAL INHIBITION AMONG PRINCIPAL NEURONS CONSTITUTE A "MOVEMENT" DETECTOR

What kind of striatal operation does occur upon a change of cortical input activity? The extensive recombination in the cortico-striatal projection is accompanied by a striking morphological homogeneity of the main receiving neuronal substrate: the principal cells. The majority of these neurons possess - apart from their projection out of the nucleus - only locally restricted axon collaterals, mainly to cells in their direct neighbourhood, i.e. within their own dendritic field (Chang et al., 1981). Thus, in sharp contrast to the situation in the cortex, the absence of long intrinsic axonal projections restricts the neostriatal activity transformation to a locally operating mechanism.

The local operation of this strongly recurrent, striatal inhibitory network will be exemplified using case number 2, considered in the previous paragraph. When neuron *a* switches in synchronization from neuron *b* to neuron *c*, the dotted area *ac* (Fig. 1) will become a newly favoured intersection domain. Such a change of temporal coherence in the cortical activity distribution can also be interpreted as a "movement" in the input, which is accompanied ("detectet") by a local change in the activity distribution in the striatum: from

the intersection(s) *ab* to the new intersection(s) *ac*. This notion of "movement detection" as a local operation occurring in the striatum helps to gain new insight into striatal function from a rather different field of study: the mechanism of movement detection in the mammalian retina. To this end, we will briefly summarize the conditions for movement detection or - more generally - for correlation detection, and will then demonstrate that these conditions are fullfilled by the striatal network.

The fundamental physiological proposal for local motion detection was made by Barlow and Levick (1965), using two input cells which were asymmetrically coupled by a delay between the input lines. In a theoretical analysis it was demonstrated that the local interaction had to be second order nonlinear (multiplication: Poggio and Reichardt, 1973). Moreover, it was shown (Torre and Poggio, 1978) that shunting inhibition approximates such multiplicative interaction, provided that two conditions are fullfilled: (1) the reversal potential of the inhibitory synapse has to overlap with the working range of the intracellular membrane potential dynamics, and (2) the shunting synapse must be close (in terms of the electrotonic length) to the excitatory synapse. Recent experiments, comparing the shunting inhibition model to other models of nonlinear interaction, demonstrated that the movement and directional sensitivity of retinal ganglion cells over a wide range of different input contrasts can indeed best be approximated by a shunting inhibition model (Amthor and Grzywacz, 1991).

As was already observed, the striatal network of principal cells is characterized by strong recurrent inhibition. Hence, the conceptual framework of "movement detection" provides quite a natural interpretation for the activity dynamics observed in striatal principal cells. Intracellular recordings in organotypic cortex-striatum co-cultures (Plenz and Aertsen, submitted) revealed *in vitro* that upon cortical, activation principal neurons stay depolarized just a few millivolts below threshold, while showing an irregular spike discharge. Such membrane potential dynamics were recently observed in principal neurons *in vivo*, where it was referred to as the "enabled state" (Wilson, 1993). It is important to note that principal neurons possess a GABAa-system with a reversal potential just below threshold, and overlapping with the membrane potential during the enabled state (Plenz and Aertsen, submitted). Thus, during this state the recurrent inhibition of principal neurons is predominantly of the shunting type. Moreover, principal neurons show a strong increase in membrane resistance upon depolarization, due to an anomalous rectifier (Wilson, 1993). This leads to an electrotonically compact dendritic tree of principal neurons during the enabled state, which strengthens the shunting operation. Upon local removal of inhibitory inputs, principal neurons start firing during the enabled state. This indicates the presence of strong inhibitory inputs stabilizing the enabled state just below threshold (Plenz and Aertsen, submitted).

In summary, we conclude that the enabled state in striatal principal neurons represents the dynamic configuration of the neostriatum to detect local correlations in the cortical activity distribution, much like the retinal network analyses the visual scene for local movement features.

"FIGURE-GROUND" DISCRIMINATION IN CORTICAL ACTVITY CHANGES

A higly simplified scheme of the local correlation detection by principal cells is outlined in Fig. 2A. This arrangement of principal cell interaction will result in output activity only if the cortical activity pattern switches from the association *ab* to the association *ac*, i.e. the input activity "moves" from A to B. However, in order to evaluate a change in the cortical activity distribution, local correlation detection is a necessary but not sufficient step. This becomes more clear when we turn once more to the metaphor of movement detection in the visual system.

Consider the situation of light points moving randomly on a screen (Fig. 2B). A single movement detector comparing two locations within the area indicated by a circle will give a certain response. This response will be high, if the movement direction of the light point within that area matches the movement orientation of the local detector (Fig. 2B, broken line). In Figure 2C, the situation for the single "local" movement detector is the same, however, a new "global" feature introduced: most of the light points on the screen move into the same direction. Clearly, local inspection of the screen does not allow to judge whether the observed local correlation results from a random distribution of moving

points (Fig. 2B) or from a global - i.e. spatially coherent - change of activity on the screen (Fig. 2C). If all movement detectors have their preferred direction of movement in parallel to the one within the circled area, this coherent pattern of moving dots will give a much larger overall response of the movement detector network than the random pattern. Obviously, the example of coherence in Figure 2C is a very simple one. Such a pattern may arise e.g. from a simple structured "figure" moving against a "ground". However, from these considerations, it is also evident that "coherence" can only be defined with respect to the underlying coordinate system of the network of movement detectors. Hence, from this point of view, single-unit studies in the neostriatum, would be of limited value to address this particular type of operation.

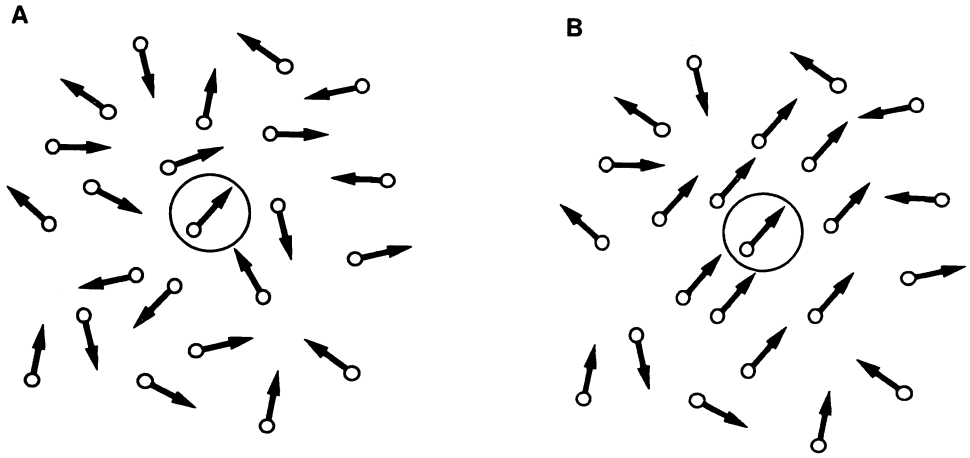

Figure 2. A. The recurrent lateral inhibition among striatal principal neurons constitutes a correlation detector. When the cortical input activity changes from *A* to *B*, this detector will give a response. If the cortical input activity would have changed from *B* to *A*, the delayed GABAa-ergic signal (Δt) from the right principal cell (ms) would have vetoed the excitatory input to the left principal cell. **glu** excitatory glutamatergic synapse from cortical afferents; **black synapse** GABAa-ergic synapse. **B.** Coherence analysis in the visual system. Light points on a retina (open circles) moving in random directions (arrows). An elementary movement detector evaluating a local region (circle) will respond to a particular movement vector (broken line). C. Similar situation as in B, but now there is a global coherence feature: light points over an extended region of space all move in the same direction. Observe that the response of the local movement detector is the same in both cases.

In summary, we conclude that in order to detect "global" coherence in the visual flow field (i.e. to extract "figure-movement" from "ground-noise"), spatial integration over the response of multiple elementary movement detectors has to be performed (Reichardt, 1987; Egelhaaf et al., 1988). Although the striatum has the anatomical appearance of a 3-dimensional volume, it functionally behaves like a 2-dimensional sheet: there is only one synapse between the main input and output structure (Wickens, personal communication). Hence, the visual analogy translates directly to the case of the neo-striatum: in order to detect "global" coherence in the "cortical flow field", spatial integration over the response of multiple elementary striatal "movement detectors" has to be performed. We propose that this extraction of global coherence in the changing cortical activity distribution is performed by spatial integration in the pallidal nuclei.

THE PALLIDAL NUCLEI AND THE SUBTHALAMIC NUCLEUS: "MINIMAL COHERENCE DETECTION"

It was shown in a quantitative anatomical study that neurons from the two pallidal nuclei integrate the activity of neostriatal principal neurons over different striatal volumes (Percheron et al., 1984). Thus, neurons from the globus pallidus externum integrate over a more restricted striatal volume than neurons from the globus pallidum internum. This view is supported by the higher burst index of neurons from the external pallidal segment as compared to that of neurons from the internal pallidal segment (Aldridge and Gilman, 1991). This arrangement of different spatial integration windows in the two pallidal nuclei not only makes it possible to detect a globally coherent change in the striatal activity, but also to extract the "spatial extent" of this coherence. We propose this to be realized in the basal ganglia by gain-controlled coupling of neurons from the globus pallidus externum to neurons from the globus pallidus internum.

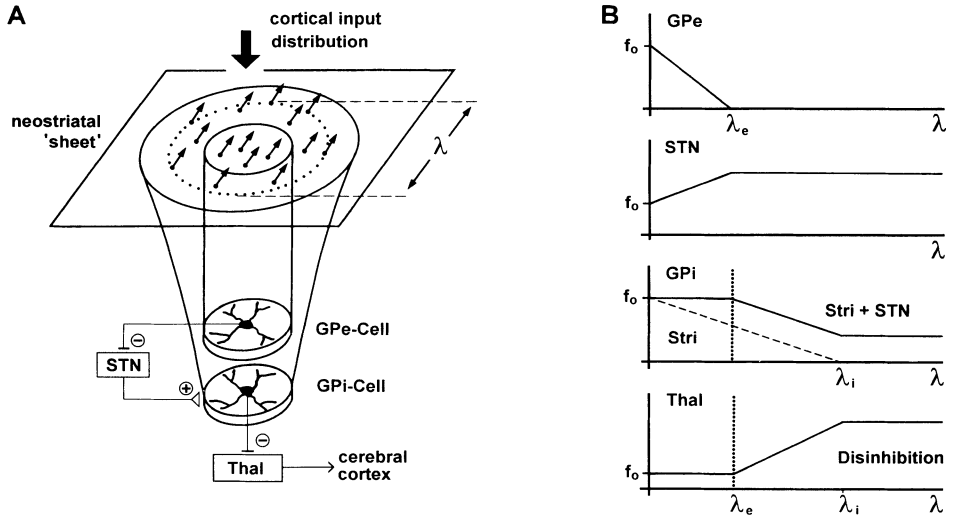

Figure 3. Minimal coherence detection. **A**. A change in the cortical activity distribution induces a certain change in the spatial pattern of activity in the neostriatal "sheet" (arrows, cf. Fig. 2). For convenience, the spatial extent of coherence is indicated as a single compact region with radius λ. Because of the smaller integration window of cells in the pallidum externum (**GPe-cell**) as compared to cells in the pallidum internum (**GPi-cell**), the inhibition exerted by the neostriatum onto a GPe-cell will saturate earlier (λe) than in a GPi cell (λi) as λ increases. **B**. The resulting decrease of GPe-cell spike activity leads to a disinhibition of the subthalamic nucleus (**STN**), which in turn increases its excitatory drive onto the GPi-cells. Consequently, the direct inhibition exerted by the neostriatum onto GPi-cells (dashed line, **Stri**) will be counterbalanced by excitation from the STN, until the extent of spatial coherence in the neostriatum exceeds the area of spatial integration of the GPe-cell (breakpoint at λe in Stri + STN curve). From here on, the activity in the GPi starts to decrease and, as a result, the disinhibitory action onto thalamic cells (**Thal**) increases. This disinhibitory action gives thalamic cells the possibility to raise cortical population activity. Thus, the STN plays a crucial role in determining the "threshold of minimal coherence" (breakpoint at λe in Thal-curve). **fo** spontaneous discharge activity.

It is known that the inhibitory and topographic pallido-subthalamic projection arises exclusively from the globus pallidus externum. The subthalamic nucleus (STN), besides having a recurrent feedback loop with neurons from globus pallidus externum, projects in an excitatory fashion to the internal pallidal segment (Parent, 1990). The sign inversion in

the projection of the subthalamic nucleus to the internal pallidal segment is necessary. We propose that this arrangement serves to evaluate whether a certain "minimal extent of coherence" is achieved, at which the basal ganglia provide a disinhibitory signal to allow the next motor program to be performed (Fig. 3). In this conceptual framework, the interaction between the two pallidal nuclei is much more than only a "balance" between two output streams of the neostriatum. It also provides a complexity judgement on the change in cortical activity distribution, the mechanism of which can be understood from the analogy of the visual systems.

The subthalamic nucleus plays a crucial role in this framework. Along the excitatory pathway from the motor cortex, a direct gain control of the action between the two pallidal nuclei can be performed (Parent, 1990). As can be easily derived from Figure 3, an increased (decreased) activity of the STN will further increase (decrease) the minimal amount of coherence necessary for exerting a certain disinhibitory action onto thalamic neurons (Bergman et al., 1990).

SELECTION OF CORTICAL CELL ASSEMBLIES BY GENERAL CONTROL OF CORTICAL POPULATION DYNAMICS

The theory developed so far requires specificity and plasticity mainly at the level of the neostriatum. There, the cortico-striatal synaptic strength, which is under dopaminergic control (Miller et al., 1990; Calabresi et al., 1992), determines the "contrast" of two cortical inputs which have to be correlated. The high plasticity of this projection is reflected by the high spine density on principal neurons. We conclude that the dopaminergic control of this plasticity can only be adequately interpreted in terms of changes in correlated input activity. The actual extraction of coherence can be reduced to a simple spatial integration, as is reflected in the uniformity of strio-pallidal synapses (DiFiglia et al., 1982).

The overall anatomy of the neostriatal/pallidal complex strongly suggests that spatial integration over local correlation detectors is used to pass a highly complex judgement on the change of the cortical activity distribution ("minimal coherence"). Nevertheless, the information carried by the coherence signal itself (e.g. in the firing rate) is low. Its real information content resides in the time at which this signal raises the general population activity in - spatially not necessarily restricted - cortical premotor and motor areas.

The specific action of an intrinsically global population dynamics signal can be understood in the framework of cortical cell assemblies. It was shown that the efficacy of synaptic coupling of a neuron onto another critically depends on the background population activity level (Aertsen and Preissl, 1991; Bernander et al., 1991). Moreover, spike activity in neurons critically depends in an expansive nonlinear way on the level of population activity (Abeles, 1982; Eeckman and Freeman, 1991). Hence, it is reasonable to conclude that pyramdidal neurons do profit differentially from a change in background population activity: upon a certain rise in population activity, neurons already receiving some synchronized excitatory inputs are more likely to discharge than neurons receiving less synchronized inputs (Abeles, 1982; Aertsen and Preissl, 1991). Thus, the selection of the motor program depends on the active linking of neurons in (pre)-motor cortices to cell assemblies currently active in other cortical areas. The selective function exerted by this activity-dependent, dynamic linking architecture mainly defines the specificity of the gating mechanism of the basal ganglia.

SUMMARY

The view of basal ganglia function developed in this paper can be described in a very short form: the formation of cell assemblies in the cortex is accompanied by spatio-temporal changes of input activity to the neo-striatum. The correlations of this input activity are evaluated under dopaminergic control in a way similar to local "movement" detection in the visual system. The very moment a certain minimal amount of coherence is detected - compare the "pop out" of "figure" from "ground" - the basal ganglia output results in a general rise of activity in cortical (pre)-motor areas, leading to a motor action. The specificity of this general rise of activity mainly emerges from the dynamic linking of neurons to currently active cell assemblies.

Acknowledgements

We thank Valentino Braitenberg, Jeff Wickens, Robert Miller, Martin Egelhaaf, Johannes Zanker and Christian Wehrhahn for helpful discussions and Volker Staiger for expert assistance in preparing the figures.

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