Neurotransmitters in the Basal Ganglia

Edith G. McGeer, William A. Staines and Patrick L. McGeer

ABSTRACT: The literature is reviewed on the afferents and efferents of the caudate/putamen, globus pallidus and substantia nigra, and on the neurotransmitters occurring in the various tracts. Emphasis is placed upon the diverse roles played by GABA and glutamate as transmitters in motor pathways and upon the probability that the substantia nigra pars reticulata plays a pivotal role in the output of the basal ganglia. Excessive stimulation of the projection from the pedunculopontine tegmental area to the substantia nigra is shown to cause destruction of dopaminergic neurons in the latter nucleus, suggesting another possible mechanism for cell death in Parkinson’s disease.

RÉSUMÉ: Nous revisons la littérature sur les afférences et efférences du caudé/putamen, globus pallidus et substantia nigra, et sur les neurotransmetteurs de ces différentes voies. Nous insistons sur les divers rôles du GABA et du glutamate comme transmetteurs des voies motrices et sur la probabilité que la substantia nigra pars reticulata joue un rôle crucial dans l’output des noyaux gris centraux. Une stimulation excessive de la projection de l’aire tegmentaire pédonculo-protubérantielle à la substance noire cause une destruction des neurones dopaminergiques dans ce dernier noyau, suggérant un autre mécanisme de mort cellulaire dans la maladie de Parkinson.


Classical neuroanatomists attempting to portray the interconnections of the extrapyramidal motor system came up with the complicated diagrams which are familiar to readers of classical textbooks. Biochemical neuroanatomists tend to reduce the complexity by showing only those tracts for which the neurotransmitter has been chemically identified. Such diagrams put undue emphasis on a few pathways. In this review we will attempt to describe the neurotransmitters of the principal nuclei of the extrapyramidal motor system in the context of the numerous tracts which have been defined by classical neuroanatomical methods and by the more recent application of axonal transport tracing techniques. The diagrams will still be oversimplified because some of the very minor tracts will be omitted and the topographical patterns which seem characteristic of many of these systems will be ignored. Possible species differences are also ignored; these are more likely to be quantitative rather than qualitative.

A complicating factor in biochemical neuroanatomy is the large number of putative transmitters in the central nervous system. These can, however, be grouped into three major classes (Table I). In general the amino acid neurotransmitters are present in micromoles/gm tissue, the amine and neuropeptides in nanomoles/gm tissue and the peptides in picomoles/gm tissue. Although glutamate, aspartate and glycine are present in many compartments other than the neurons they serve, it still seems probable that the amino acids must account for a very high proportion of the neurons of brain. The other neurotransmitters may, of course, by their modulatory actions, have qualitative importance far outweighing their probable quantitative importance. It is clear, however, that the probable quantitative importance of the various neurotransmitters in brain is not well correlated with the priorities that have been given in research or with the amounts of knowledge accumulated. Thus, a major part of neurotransmitter-related research in the last 25 years has been directed towards the aromatic amines and the peptides are now enjoying a tremendous surge in popularity. Considerable knowledge of the neuroanatomy of these systems has been accumulated and most speculation as to the relation of disease or function to specific neurotransmitters has been focused on the amines and peptides. Although the amino acids are favorites of the neurophysiologists — since they seem to act by classical ionic mechanisms — they have been neglected until relatively recently by the neuroanatomists, neuropsychologists and clinically oriented neuroscientists.

Most of the neurotransmitters listed in Table I are present in the extrapyramidal system, many of them in relatively high

<table>
<thead>
<tr>
<th>AMINO ACIDS</th>
<th>AMINES</th>
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<tr>
<td>(70-90% of central neurons)</td>
<td>(5-20% of central neurons)</td>
</tr>
<tr>
<td>*Glutamate 14,000,000</td>
<td>Acetylcholine 25,000</td>
</tr>
<tr>
<td>Aspartate 4,000,000</td>
<td>Dopamine 6,500</td>
</tr>
<tr>
<td>*GABA 2,500,000</td>
<td>Noradrenaline 2,500</td>
</tr>
<tr>
<td>*Glycine 2,000,000</td>
<td>Serotonin 2,500</td>
</tr>
<tr>
<td></td>
<td>Histamine 1,000</td>
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</tbody>
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PEPTIDES (Partial List) (less than 5-10% of central neurons)

| CCK 470 | LHRH 7 |
| Met-enkephalin 350 | Dynorphin 4 |
| Substance P 100 | Bradykinin <1 |
| VIP 40 | ACTH <1 |
| Somatostatin 30 | α-MSH <1 |
| Neurotensin 12 | TRH <0.3 |
| | Bombesin <0.2 |

* Present in the basal ganglia

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concentrations compared to other brain regions. In discussing
where these neurotransmitters may fit into the wiring diagrams
of the extrapyramidal system, these will be considered in terms of
the efferents and afferents of the caudate/putamen (CP), of
the globus pallidus (GP) and of the substantia nigra (SN).

Projections of the Caudate/Putamen (See Figure 1)

The projections of the CP are simple since there appear to be
only three, or possibly four. Well established tracts are those to
the GP, the entopeduncular nucleus (EP) and the SN (Dray,
1979; Beckstead (1983) and Nauta and Cole (1978) indicate a
minor projection to the subthalamus. The projection from the
CP to the SN is particularly massive and probably ends mainly
in the zona reticulata (SNR) (Hattori et al., 1975). As many as
65-70% of the neurons of the CP may project to the SN and at
least two morphologically distinct types of striatonigral neurons
have been shown (Bolam et al., 1981).

Five neurotransmitters have so far been implicated in these
projections. There is excellent evidence for enkephalin as a
neurotransmitter in projections from the CP to the GP (Brann
and Emson, 1980; Del Fiacco et al., 1982; Somogyi et al., 1982;
cf Haber and Elde, 1981). The CP contains a dense network of
met-enkephalin fibers and terminals (Yang et al., 1983) so there
may also be enkephalin interneurons.

Substance P projections arise throughout the CP and seem to
project, probably by collaterals, to all three other nuclei, i.e. to
the GP, the EP and the SN (Brownstein et al., 1977; Jessel et al.,
1978; Staines et al., 1980). In primates, the external segment
(GP) shows relatively little staining for substance P, with the
staining being, progressively, much more dense in the internal
segment (EP) and in the SN (Beach and McGeer, 1984; Haber
and Elde, 1981). Substance P, enkephalin and acetylcholinesterase
have all been found to occur in different, distinct patterns in the
cat caudate, with more uniform patterns in the putamen (Graybiel
et al., 1981). Islands of intense substance P-like immunoreactivity
have also been found in human and baboon caudate (Beach and

Dynorphin distributions are similar to those of substance P
(Vincent et al., 1982a) and this endorphin may occur in similar
projections to all three nuclei; that to the SN is the best established
(Vincent et al., 1982b).

GABA occurs in a massive projection from the neostriatum
to the SN but it is controversial as to whether the greater part of
this projection arises in the GP, the tail of the caudate or at the
border between the two (for review see E.G. McGeer et al.,
1982). There are also GABA projections from the CP to the GP
and from the CP to the EP. The GABA projections to the GP
may be partly by collaterals of those to the SN.

Cholecystokinin (CCK) may also be present in a projection
to the SN since injections of the neuropeptide, kainic acid, into
the rat CP lead to losses of CCK in the SN as well as the CP
(Emson et al., 1980; see also Table 3).

Afferents to the Caudate/Putamen (See Figure 2)

The most massive inputs come from the thalamus, the cortex
and the SN. There are also minor inputs from the locus coeruleus,
the dorsal raphe, the amygdala, probably the mammillary body,
pedunculopontine tegmental nuclei and, possibly, the reticular
formation and subthalamus. The projections from the SN and
the raphe are both reported to be partly to the contralateral CP
but the same cells do not project bilaterally (Loughlin and
Fallon, 1982). The prefrontal and SN projections to the CP are
convergent (Beckstead, 1979).

A major unsolved question in the biochemical neuroanatomy
of the extrapyramidal system is the nature of the neurotrans­
mittser(s) in the massive thalamostriatal tract. Despite some
reports, it appears highly unlikely that this tract is served
largely by glutamate, aspartate or acetylcholine (P.L. McGeer
et al., 1982; McGeer et al., 1977).

The relatively minor projections from the dorsal raphe and
locus coeruleus are parts of the well-known and diffuse
serotonergic and noradrenergic systems of the brain. A second
(excitatory) neurotransmitter may be involved in the raphe­
striatal tract (Park et al., 1982).

There is some lesion evidence indicating that histamine
innervation of the CP arises in the mammillary body and possibly
also in the reticular formation (Barbin et al., 1977).

The well-known dopamine system from the SN to the CP also
gives off some collaterals in the GP. Although dopamine probably
accounts for about 85-95% of the massive nigrostriatal tract,
there does seem to be at least one other neurotransmitter involved
(Connor, 1975; Deniau et al., 1978b; Fibiger et al., 1972; Hedreen,
for a minor role in this tract is neurotensin. Neurotensin
immunoreactive cells are found in the SN (Jennes et al., 1982;
Uhl et al., 1979), there is a dense mosaic of positive fibers and
terminals in the striatum (GP > caudate > putamen) (Goedert
et al., 1983), and neurotensin facilitates dopamine release in

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**Figure 1 — Projections of the Caudate/Putamen. In this and subsequent diagrams,
relative sizes and locations of the nuclei are ignored and a given tract may
involve more than the neurotransmitters shown. For the topography of the
projection to the GP, see Wilson and Phelan (1982) and Chang et al.
(1981), and for the morphology of cells projecting to the SN, see Smith
et al. (1981) and Tulloch et al. (1978). Enk, enkephalin; SP, substance P;
Dy, dynorphin; other abbreviations as in text.**

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[Dy, dynorphin; other abbreviations as in text.](https://www.cambridge.org/core/terms)
Figure 2 — Afferents to the Caudate/Putamen. (a) GP to CP (Staines et al., 1981; Arbuthnott et al., 1982a,b; Buchwald et al., 1981; Chung and Hassler, 1982; Jayaraman, 1983 (topography)). (b) Tegmental area to CP (Saper and Loewy, 1982). (c) Cortex to CP (Hedreen, 1977; Vetnerian and van Heesijn, 1978; Fallon and Ziegler, 1979; Oka, 1980; Donoghue and Kitai, 1981; Royce, 1982). (d) Thalamus to CP (From intralaminar (IL) and parafascicular (PF) nuclei; projections from the ventromedial nucleus (VM) are controversial (Jones and Leavitt, 1975; van der Kooy, 1979; Veening et al., 1980; Herkenham, 1979; DiFiglia et al., 1978; Sugiarto and Hattori, 1983 (collaterals to the subthalamicus)). (e) Amygdala to CP (Royce, 1978; Kelley et al., 1982). (f) Raphe to CP (van der Kooy, 1979; Loughlin and Fallon, 1982). (g) Subthalamus to CP (sparse and may be to displaced GP cells. Ricardo, 1980; van der Kooy and Hattori, 1980). Glu, glutamate; HIS, histamine; NA, noradrenaline; 5HT, serotonin; DA, dopamine.

vitro from striatal slices (de Quidt and Emson, 1983). The levels are generally reported as relatively high in both the CP and SN although there is some variability in the available data (Goedert and Emson, 1983; Emson et al., 1982; Manberg et al., 1982; Uhl and Snyder, 1976).

It is also remotely possible that CCK may be involved in the nigrostriatal projection but the majority of the CCK innervation of the CP seems to come from the amygdala (30%) and the pyriform cortex and/or claustrum (70%) (Meyer et al., 1982).

The projection from the amygdala to the CP may also contain somatostatin. Other suggested sources of somatostatin innervation of the CP are the cortex, the periventricular nucleus of the hypothalamus and the tegmental area since somatostatin-positive cells have been reported in those locations (Takatsuki et al., 1981). Beal and Martin (1983) indicate that about half of the somatostatin in the CP comes from external sources but not from the dorsal cortex, thalamus or brainstem. The other half of the somatostatin in the CP appears to be in perikarya which are probably intrinsic neurons (DiFiglia and Aronin, 1982; Finley et al., 1978; Graybiel et al., 1981). It has been estimated that 4-5% of striatal neurons in a rat contain somatostatin and these are distinct from the 4 to 5% which are intrinsic cholinergic neurons (Vincent et al., 1983a); some of the somatostatin cells also contain avian pancreatic polypeptide (APP)-like immunoreactivity (Vincent et al., 1982c). As seems to be the case for most neurotransmitters, there are anterior to posterior variations in somatostatin levels in all nuclei of the basal ganglia (Davies et al., 1981) and the staining of cells is found in patches in the CP (Chesselet et al., 1982; DiFiglia and Aronin, 1982).

The pallido-striatal tract appears to be GABAergic and to land largely on the somatostatin neurons. There are also, of course, many GABA interneurons in the CP, as well as some thyrotropin releasing hormone (TRH) perikarya (Spindel et al., 1981). Relatively little is known about the TRH system.

The massive projection from the cortex to the CP appears to use glutamate and/or aspartate — what we prefer to call a Glu/Asp system since it is sometimes difficult to distinguish the one from the other (although the evidence in this particular case favors glutamate as the neurotransmitter). This excitatory system innervates most of the neurons of the CP and there are similar cortical Glu/Asp projections to other subcortical areas related to motor control including the ventrolateral thalamus, the red nucleus, the basis pontis, the superior colliculus, the spinal cord and probably the SN and subthalamus (Figure 3).

The Glu/Asp projection to the CP comes mainly from the neofrontal, motor and pyriform areas of the ipsilateral cortex but there is some contribution from the contralateral cortex; this is one of the levels at which some integration between the hemispheres may occur (Leichnetz, 1981; Walker, 1983). Since many commissural pathways are also probably Glu/Asp, such integration is highly dependent upon these amino acid transmitters.

An interesting possibility suggested by work in other areas of brain is that adenosine receptors may be located on axon terminals of these excitatory Glu/Asp neurons and help regulate the output of the excitatory neurotransmitter (Goodman et al., 1983; Wojcik and Neff, 1983).

Figure 3 — Glu/Asp projections to some nuclei possibly or probably concerned in motor control. For reviews of the literature on these pathways see McGeer and McGeer, 1981; Walker, 1983.
Afferents to the Globus Pallidus (see Figure 4A)

Two of the main afferents have been previously described and comprise inputs from the CP and from the SN. The input from the CP contains enkephalin and probably GABA; some substance P and dynorphin fibers may also occur. The projection from the SN certainly contains dopamine and may contain other substances.

Projections to the GP also arise in the subthalamus, the nucleus accumbens and, possibly, the tegmental area (see last page of text). The transmitter serving the tract from the subthalamus is still uncertain since it has been variously reported to use the inhibitory transmitter GABA or to be excitatory; this projection is believed to have collaterals to the SN and EP (Deniau et al., 1978a; van der Kooy and Hattori, 1980a). The projection from the nucleus accumbens — which may be considered a ventral extension of the CP — is to the ventral pallidum rather than the GP proper and seems to use GABA (see Figure 5).

Projections of the Globus Pallidus (see Figure 4B)

The GP projects mainly to the subthalamus (Kim et al., 1976) but also the EP, the SN (Hattori et al., 1975; Carter and Fibiger, 1978), the CP, the dorsal raphe and, rather sparsely, to the

Figure 4 — Afferents to the Globus Pallidus (A) and Projections from the Globus Pallidus (B). Rt, reticular and MD, medial dorsal nuclei of the thalamus; other abbreviations as in Fig. 1.

Figure 5 — Reported axoned GABAergic tracts. Many references may be found in E.G.McGeer et al. (1982); McGeer and McGeer (1981). cf also: (a) EP to lateral habenula, Contestible and Fonnum (1983) who also report a GABA projection from the diagonal band of Broca to the medial habenula. (a,b) The projections from the rostral EP and the lateral hypothalamus to the lateral habenula apparently arise from both GABAergic and non-GABAergic cells (Araki et al., 1984b). (c) Subthalamus (SUT) to EP, Rouzaire-Dubois et al. (1983). (d) Scarnati et al. (1983). (e) Vincent et al. (1983b). (f) Strarr and Kilpatrick (1981); no convergence of pallidal and nigral influences is observed within thalamic neurons (Ueki, 1983). (g) Chevalier et al. (1981a,b); double labelling studies indicate that the projection to the superior colliculus from the pars reticulata of the SN (and from the nearby zona incerta) are wholly GABAergic (Araki et al., 1984a). (h) Childs and Gale (1983), diffuse GABA projections to pedunculopontine nucleus and adjacent tissue of the pontomesencephalic tegmentum. (i) EP to VL thalamus; these projections are partially bilateral (Nakano et al., 1982; DeBellefeuille and Parent, 1982). (k) Both the GP to CP and CP to GP paths send some collaterals to the SN. (l) Scatton et al. (1982).
reticular and medial dorsal nuclei of the thalamus and to the frontal cortex (Nauta, 1979a).

There have been claims of a pallidocortical cholinergic projection (Edstrom and Phillips, 1980; Kelly and Moore, 1980), but this projection arises from the magnocellular neurons of the substantia innominata (nucleus basalis of Meynert), the distribution of which overlaps the boundaries of the globus pallidus (and putamen). Another projection, from non-magnocellular cells of the GP proper, is limited to the frontal cortex (Ribak and Kramer, 1982); the neurotransmitter is unknown but may be GABA.

GABA is the only neurotransmitter yet definitively identified in any of the projections of the GP. The GP, like the EP and the SN, probably contains a very high concentration of GABAergic neurons. In histochemical studies in our laboratory aimed at identifying presumptive GABAergic neurons, some of the most beautiful staining was evident in these three nuclei (Nagai et al., 1983). These nuclei are also prominent in Figure 5 which shows almost all of the long axoned GABA systems which have been so far suggested in the literature. In addition, most of the nuclei shown in Figure 5 contain high concentrations of GABA interneurons. It is clear that GABA systems play a major role in motor control but act at many different levels.

A number of these pathways are believed to be extensively collateralized and some appear to converge. Thus, for example, the EP to the thalamus innervates the same ventromedial nucleus (Carter and Fibiger, 1978) that receives innervation from the SN (Clavier et al., 1976) and from the deep cerebellar nuclei (Herkenham, 1979; Sugimoto et al., 1981) and projects in turn to cortical regions which innervate the CP (Herkenham, 1979). Some recent lesion studies in our laboratory indicate that at least part of the ipsilateral projection from the pedunculopontine nuclei (peribrachial area) may be cholinergic but that another neurotransmitter is probably involved in the bilateral projections. Cholinergic neurons are located diffusely in this general area (Kimura et al., 1981, 1984) and microinjections of the excitotoxin, ACh, acetylcholine; OXY, oxytocin; AVP, vasopressin; other abbreviations as in Fig. 1.

Afferents to the Substantia Nigra (see Figure 6)

The SN is the smallest of the nuclei of the extrapyramidal system which we are considering but seems nevertheless to have the most complicated wiring diagram. These involve a number of connections with the contralateral side which provide, with the bilateral cortical innervation of the striatum and the commissural Glu/Asp tracts, means for hemispheric integration. Major afferents to the SNR and zona compacta (SNC) which come, respectively, from the CP and the GP have already been discussed. There is also a projection from the nucleus accumbens to the SNC and from the midbrain tegmental area, most probably the pedunculopontine nucleus, to the SNR and SNC. The latter projection is bilateral, although the ipsilateral component is much heavier than the contralateral component. The SN also receives projections from the cortex, the lateral habenula, the parafascicular nucleus of the thalamus, the subthalamus, the amygdala, the raphe and the hypothalamus. All of these seem to be exclusively ipsilateral except for the hypothalamic afferents which are bilateral. However, those from the ipsilateral hypothalamus come from the anterior portion, while those from the contralateral come from the posterior regions. The transmitters for many of these afferents are unknown but some have been postulated.

Some of the probable transmitters in the tracts from the cortex, the CP, the GP and the raphe have already been mentioned, i.e.: from the raphe, serotonin; from the CP, substance P, GABA and dynorphin; from the GP, probably GABA; and from the cortex possibly glutamate and/or GABA (see Figures 3 and 5).

It has been said that some oxytocin and a few vasopressin fibers project to the SN from the hypothalamus (Nilaver et al., 1979; Sofroniew, 1980). Some recent lesion studies in our laboratory indicate that at least part of the ipsilateral projection from the pedunculopontine nuclei (peribrachial area) may be cholinergic but that another neurotransmitter is probably involved in the bilateral projections. Cholinergic neurons are located diffusely in this general area (Kimura et al., 1981, 1984) and microinjections of the excitotoxin,

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**Figure 6 — Afferents to the SN.** For references see Gerfen et al. (1982) and Saper and Loewy (1982). ACh, acetylcholine; OXY, oxytocin; AVP, vasopressin; other abbreviations as in Fig. 1.
kainic acid, caused local lesions which did not encroach upon the SN (or the midline) but which, nevertheless, resulted in significant decreases in both glutamate decarboxylase (GAD) and choline acetyltransferase (ChAT) levels in the ipsilateral SN. These enzymes were not affected in the contralateral SN or in either CP. Pretreatment with scopolamine abolished the changes in GAD without affecting those in ChAT (Table 2A). These results are consistent with an ipsilateral cholinergic projection from the injected region to the SNR, with the loss of GAD in the SNR being a secondary effect dependent upon overexcitation of this projection. Such an effect would be analogous to the loss of cortical and amygdala GABA neurons seen following injections of either kainic acid or folic acid into the substantia innominata area where the cholinergic innervation of cortex and amygdala arises (McGeer et al., 1983). The postulated mechanism for the loss of GAD in the SN is consistent with the reports that acetylcholine is markedly excitatory to cells in the SNR (Collingridge and Davies, 1981; Pinnock and Dray, 1982).

Such injections of kainic acid (or folic acid) also caused losses of dopamine cells in the SN (as initially reported by Ricciardi et al., 1981); these losses were partly bilateral as evidenced by measurements of tyrosine hydroxylase in the CP (Table 2B) and were not significantly affected by scopolamine. This suggests that the bilateral projection from this area innervates dopamine neurons of the SN and is served by some transmitter other than acetylcholine. One possibility is the excitatory peptide, neotensin, since its levels are relatively high in the SN, the neurotensin binding sites are said to be on dopamine neurons (Palacois and Kuhar, 1981) and neurons straining for neotensin have been found in the dorsal pontine tegmental area (Matsuzaki et al., 1981; Beitz, 1982). Substance P is another possibility since it is excitatory and ascending projections from this general area have been reported (Sakanaka et al., 1983).

It is tempting to speculate that abnormalities in these projections and assessing their status in Parkinsonian brains seems worthwhile.

Almost certainly other transmitters are also involved in afferents to the SN. Histamine concentrations, histidine decarboxylase activity and high affinity glycine uptake are all relatively high in the SN, suggesting the possibility of afferents or internal neurons using these neurotransmitters. Pollard et al. (1978) indicated there were most probably histamine afferents to the SN but the origin was unknown.

**Projections from the Substantia Nigra (see Figure 7)**

The projections from the SN are equally complex. There is a vast literature on the massive projections to the CP and to the ventromedial nucleus of the thalamus. There are much less data

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**Table 2: Some enzyme levels (as percent of control) following injections of kainic acid or folic acid into the pedunculopontine tegmental area**

<table>
<thead>
<tr>
<th>A. In the Substantia Nigra</th>
<th>ChAT</th>
<th>GAD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ipsi</td>
<td>Contra</td>
</tr>
<tr>
<td>Kainic acid (KA) injected</td>
<td>51%* 86%</td>
<td>59%* 96%</td>
</tr>
<tr>
<td>KA after scopolamine</td>
<td>49%* 81%</td>
<td>97% 109%</td>
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<tr>
<th>B. In the Neostriatum</th>
<th>Tyrosine Hydroxylase</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ipsi</td>
</tr>
<tr>
<td>Folic acid injected</td>
<td>74%* 92%</td>
</tr>
<tr>
<td>KA injected</td>
<td>64%* 82%*</td>
</tr>
<tr>
<td>KA after scopolamine</td>
<td>80%* 84%*</td>
</tr>
</tbody>
</table>

* Significantly different from control; the tyrosine hydroxylase values in the last two groups are not significantly different one from the other.
on the massive but somewhat diffuse projection to the tegmental area. The SN also projects to the subthalamus, the parafascicular, ventromedial, medial dorsal and lateral dorsal nuclei of the thalamus, the amygdala, the olfactory bulb, the superior colliculus, the midbrain and pontine central grey and the spinal cord. The projections to the superior colliculus, various thalamic nuclei and the midbrain and pontine central grey are bilateral, with the ipsilateral innervation being the more massive in each case.

Only two neurotransmitters, dopamine and GABA, have so far been identified in projections from the SN. There are dopaminergic tracts to the CP, GP, amygdala (Meibach and Katzman, 1981), subthalamus (Brown et al., 1979; Miebach and Katzman, 1978), olfactory bulb and spinal cord; a dopaminergic tract to the hypotalamus has been suggested (Mannisto et al., 1981) but there seems little evidence for such a projection.

GABA is a transmitter in the projections to the superior colliculus and the thalamus and some of these are collaterals (Bentivoglio et al., 1979; Anderson and Yoshiha, 1980). GABA is also contained in the projections to the tegmentum and one group has estimated from physiological studies that some 40% of nigral neurons send inhibitory fibers to the tegmentum with about half of these having collaterals to either the thalamus and/or the superior colliculus (Nijima and Yoshiha, 1982; Beckstead and Frankfurter, 1982). Collaterals within the SN of these projection neurons have also been suggested (Grofova et al., 1983) is in keeping with electron microscopic evidence reviewed in such studies is beyond the scope of this paper but...
Figure 8 — A hypothetical diagram of information flow in the basal ganglia. Thal+ stands for all regions projecting to the CP except the cortex and SNC.

(Araki et al., 1984a) Presumptive GABAergic pathways from the midbrain to the superior colliculus studied by a combined HRP-GABA transaminase pharmacohistochemical method. Neuroscience, in press.


REFERENCES


