

## Sensory projections to the nucleus basalis prosencephali of the pigeon

Ulrich Schall, Onur Güntürkün, and Juan D. Delius

Experimentelle Tierpsychologie, Psychologisches Institut Ruhr-Universität Bochum, Bochum, Bundesrepublik Deutschland

**Summary.** The afferent pathways to the nucleus basalis prosencephali of the pigeon were studied by use of the horseradish peroxidase (HRP) technique. It was confirmed that this nucleus receives a direct pathway from the nucleus sensorius principalis nervi trigemini and that, as in the starling, it receives a direct input from the nucleus lemnisci lateralis, pars ventralis, an auditory relay. Totally novel is the finding that the nucleus basalis prosencephali is the target of a direct pathway originating in the medullary nucleus vestibularis superior. All three pathways bypass the thalamus. From within the telencephalon the nucleus basalis prosencephali also receives fibres from the tuberculum olfactorium and the peri-ectostriatal belt, suggestive of olfactory and visual input. Marked cell bodies were also found in the neostriatum frontolaterale. It is assumed that these arose from HRP uptake by axons of the tractus fronto-archistriatalis that course through the nucleus basalis prosencephali to the anterodorsal archistriatum. Marked fibres and bouton-like formations were observed in the latter structure. The afferents to the nucleus basalis prosencephali are discussed in conjunction with the probable role of the nucleus as a sensorimotor coordinator of the pecking/feeding behaviour of the pigeon.

**Key words:** Nucleus basalis prosencephali – Feeding system – Sensorimotor circuit – Retrograde tracing – Pigeon

The nucleus basalis prosencephali (Bas) is a salient feature of the frontal forebrain of birds. In 1903 Wallenberg discovered that the Bas of birds receives a direct projection from the nucleus sensorius principalis nervi trigemini (PrV) via the tractus quintofrontalis (QF), bypassing the thalamus (see also Wallenberg 1966; Dubbeldam et al. 1981; Wild et al. 1984). Later electrophysiological work (Witkovsky et al. 1973; Berkhoudt et al. 1981) showed that the Bas receives short latency (4–8 ms) somatosensory input from the beak area. Additionally, Iljitshev and coworkers (Naumov and Iljitshev 1964; see also Harman and Phillips 1967) recorded short latency (5–8 ms) auditory-evoked potentials from the Bas area. These latter findings were initially disregarded by other workers as artefacts (Karten 1969) but a study incorporating various control procedures proved

Send offprint requests to: Dr. Onur Güntürkün, Psychologisches Institut, Experimentelle Tierpsychologie, Universitätsstr. 150, D-4630 Bochum 1, Federal Republic of Germany

the auditory potentials to be genuine, cochlearly driven responses (Delius et al. 1979; see also Berkhoudt et al. 1981). Kirsch (1983) mentioned that in the starling (*Sturnus vulgaris*) the auditory pathway has its origin in the nucleus lemnisci lateralis, pars ventralis (LLv), itself an auditory nucleus (Boord 1968).

Brain lesion (Zeigler 1976), electrical stimulation (Delius 1971) and, more recently, chemical stimulation and metabolic labelling studies (Delius 1985) suggest that the Bas is involved in the control of feeding or more precisely in the control of pecking, grasping and swallowing. It is known that the neostriatum frontolaterale (NFL) in the neighbourhood of the Bas projects via the tractus fronto-archistriatalis (FA) to the anterior archistriatum (A) (Veenman 1984; Wild et al. 1984, 1985) and that the archistriatum in turn projects via the tractus occipitomesencephalicus (OM) to a variety of di-, mes-, rhombencephalic and spinal structures (Zecha 1962; Zeier and Karten 1971; Berkhoudt et al. 1982). At least one of these structures has motor functions related to pecking. Berkhoudt et al. (1982) established that a mesencephalic target of the OM, the nucleus reticularis parvocellularis, pars lateralis (Rpv) projects to the nucleus motorius nervi trigemini (MV) and nucleus nervi facialis (nVI). These innervate the musculature of the beak (Wild and Zeigler 1980).

We now report results of a horseradish-peroxidase injection study. It shows that the Bas of the pigeon receives further sensory afferents, in addition to those mentioned above. These fit its role as a sensorimotor coordinator of the pecking response of the pigeon.

### Materials and methods

Eight adult homing pigeons (*Columba livia*) with body weights of 450–600 g were used. While the birds were anaesthetized, 0.1–0.3 µl of 30–40% horseradish peroxidase (HRP, Sigma VI) in 0.9% saline solution were injected into the brain with the use of a Hamilton microsyringe via a glass microcapillary with a 40-µm diameter tip under stereotaxic guidance. The microcapillary remained in the brain for 30 min after the injection. The survival time for all pigeons was 24 h. The composition and dosage of the anaesthetic used, a chloral hydrate-pentobarbital mixture, is described by Mallin and Delius (1983).

The animals were perfused intracardially under anaesthesia with 500 ml 0.9% saline solution (40° C) followed by 500 ml fixation solution consisting of 1% paraformaldehyde

hyde and 1.25% glutaraldehyde in 0.12 M sodium phosphate buffer (pH 7.4, 20° C). Following fixation, 500 ml 10% saccharose in 0.12 M sodium phosphate buffer solution (pH 7.4, 4° C) was used to flush out excess aldehydes. The brains were immediately removed from the skulls and cut sagittally on a freezing microtome in steps of 40 µm. The sections were collected in 0.12 M sodium phosphate buffer solution (pH 7.4) and incubated for visualisation with tetramethylbenzidine (TMB Sigma) according to the procedure described by Mesulam (1978). Then, the sections were mounted on slides, dried for 12 h at 35° C, counterstained with 0.1% neutral red, cleared in a series of graded alcohol (15–17 sec in each of 70%, 96% and 2 × 100% solutions) and in xylol (5 min), and coverslipped. Sections of brains from control pigeons stained with Nissl or Nissl/myelin staining and the atlas of Karten and Hodós (1967) aided the identification of anatomical structures in the HRP-stained sections.

## Results

In three of the eight pigeons the detectable deposits of the HRP-injections were exclusively restricted to the nucleus basalis prosencephali (Bas). In one pigeon the injection was placed in the neostriatum frontolaterale (NFL), rostral to the Bas. In another pigeon the Bas and the NFL were equally marked with HRP and in two pigeons the HRP-deposits diffused slightly from the Bas into the paleostriatum augmentatum (PA).

Injections that involved the Bas lead to labelling of cell bodies and axons in the telencephalon and in the rhombencephalon. The areas labelled in these two brain structures will be described separately. Following injection in the NFL, rostral to the Bas, only labelled neurones in the Bas could be detected. Under this condition no labelled structures could be observed either in the telencephalon or in the rhombencephalon.

### Telencephalon

Following HRP-injections into the Bas, numerous neurones with a diameter of perikaryon of 9–15 µm were consistently labelled in the ipsilateral NFL (Figs. 1, 2). The retrogradely filled axons of these cells course in parallel fascicles to the Bas (Fig. 3). Posterior to the Bas, HRP-positive axons lead via the tractus fronto-archistriatalis (FA) to the frontal parts of the ipsilateral archistriatum and the neostriatum directly overlying it (Fig. 4). Since bouton-like knobs were observed on the terminations of these axons, it is assumed that HRP labelled the FA in an anterograde manner (Fig. 5). To check whether the axons of the FA originate

in the Bas or the NFL, the sections of a pigeon from a previous unpublished HRP-study were reexamined. The animal received an HRP-injection in the most anterior portion of the archistriatum, bordering on the overlying neostriatum. This injection labelled numerous neurones in the NFL but no HRP-positive cells could be detected in the Bas. In accordance with the results of Wild et al. (1984, 1985) it is concluded that the neurones of the NFL project via the FA through the Bas to the anterior portions of the ipsilateral archistriatum. Our injections into Bas apparently interrupted this projection and lead to anterograde labelling of the Fa and to retrograde labelling of the NFL-neurones.

The injections into the Bas lead to the labelling of neurones in the anterior part of the paleostriatum augmentatum at the border to the Bas and in two further, more distinct ipsilateral telencephalic regions: the tuberculum olfactorium (TO) and the peri-ectostriatal belt (Ep). The neurones of the tuberculum olfactorium with a diameter of 7–11 µm were observed in the ventromedial part of the telencephalon. The HRP-positive ectostriatal neurones were detected in the medial part of the peri-ectostriatal belt corresponding approximately to the sagittal level L 3 Karten and Hodós' atlas (Fig. 6). The axons of these neurones could be traced running along the lamina medullaris dorsalis (LMD) into the Bas. All intratelencephalic afferents and efferents are shown in Fig. 7.

### Rhombencephalon

HRP-injections into any part of the Bas always lead to heavy bilateral labelling of neurones in the lateral half of the nucleus sensorius principalis nervi trigemini (PrV, Figs. 8, 9). Only injections in the most lateral Bas yielded some HRP-positive cells in the medial PrV. This projectional pattern of the PrV upon the Bas confirms the observations in the duck of Dubbeldam et al. (1981), who demonstrated that the medial and lateral areas of the PrV, which receive afferents from the ramus mandibularis nervi trigemini project to the medial parts of the Bas. Afferents from the ramus maxillaris reach the medial PrV and project from there to the lateral regions of the PrV. The numbers of labelled cells in the PrV ipsi- and contralateral to the injection side were similar. The perikaryon diameter of the HRP-positive cells was about 8–11 µm.

After HRP-injections into the Bas, labelled cells were also observed in the contralateral nucleus vestibularis superior (VS). The location of these sparsely distributed neurones with a perikaryon diameter of 8–15 µm ranged from the dorsal border of the PrV to the ventral extent of the brachium conjunctivum (Figs. 10, 11).

In agreement with the findings of Kirsch (1983) in the

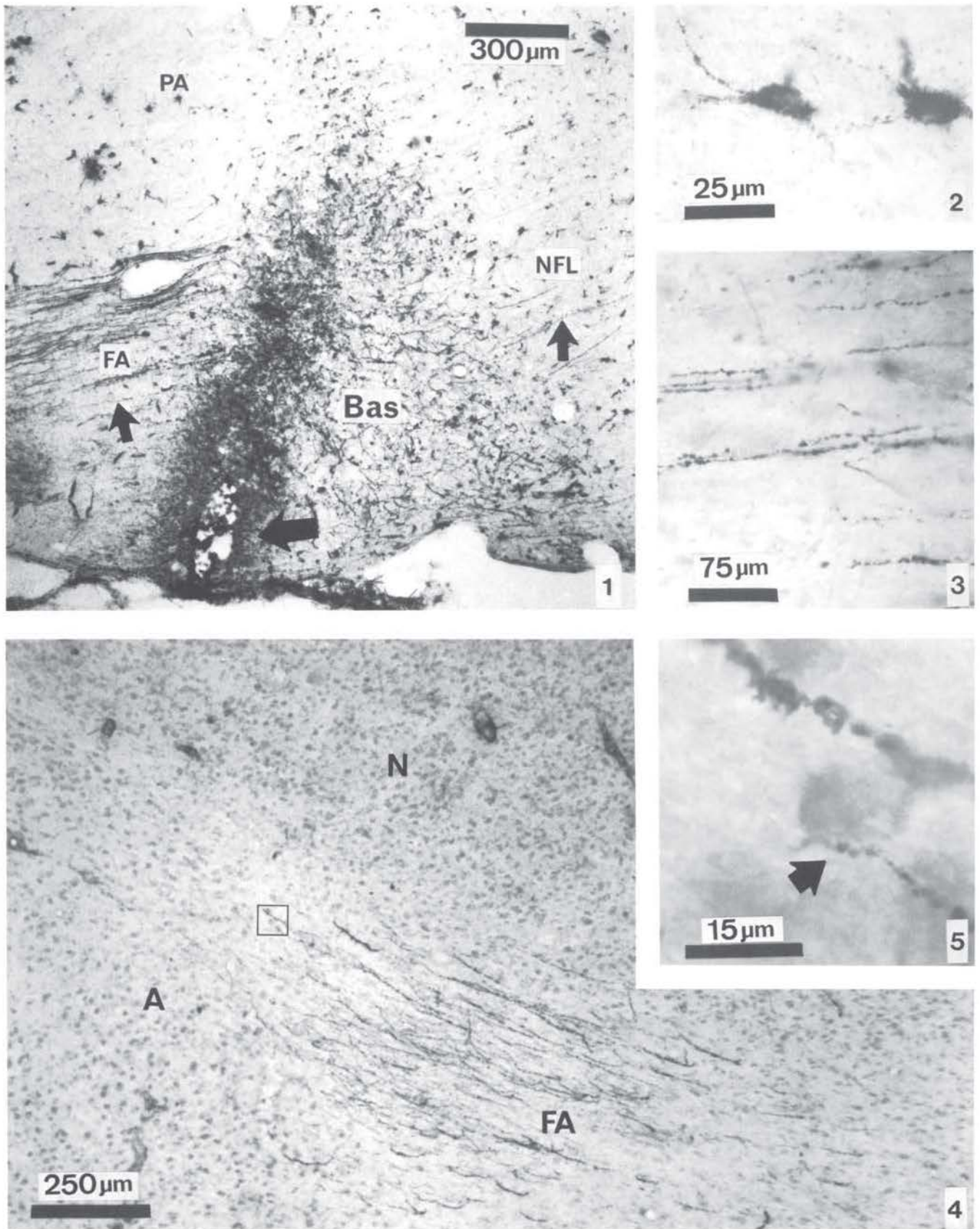
**Fig. 1.** HRP-injection into the nucleus basalis prosencephali (Bas) (*large arrow*). Retrogradely labelled, parallel fibres and HRP-positive neurones (*small arrow on the right*) are visible in the NFL. A portion of the anterogradely labelled FA can be seen coursing caudally (*small arrow on the left*). The section corresponds to the L 3.50 plane of the Karten and Hodós (1967) atlas. Bas nucleus basalis, FA tractus fronto-archistriatalis, NFL neostriatum frontolaterale, PA paleostriatum augmentatum. × 56

**Figs. 2, 3.** Retrogradely labelled neurones and axons in the NFL after an HRP-injection into the Bas. × 595 and × 200, respectively

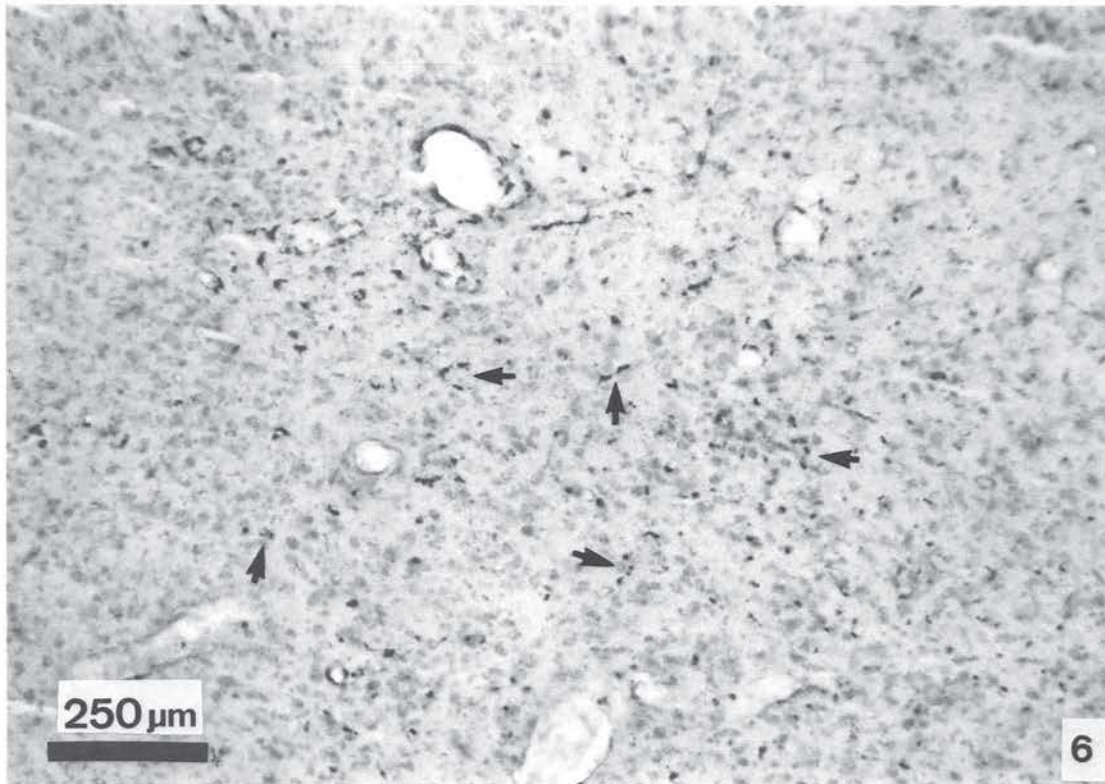
**Fig. 4.** Following an HRP-injection into the Bas anterogradely labelled fibres of the FA can be seen reaching the anterior portion of the archistriatum. The section corresponds to the sagittal plane L 6.25 of the Karten and Hodós atlas (1967). × 74. The *small square* is shown magnified in Fig. 5. A archistriatum, N neostriatum; see also Fig. 1

**Fig. 5.** Enlargement of a portion of Fig. 4 showing end-boutons of the FA fibres. × 1250

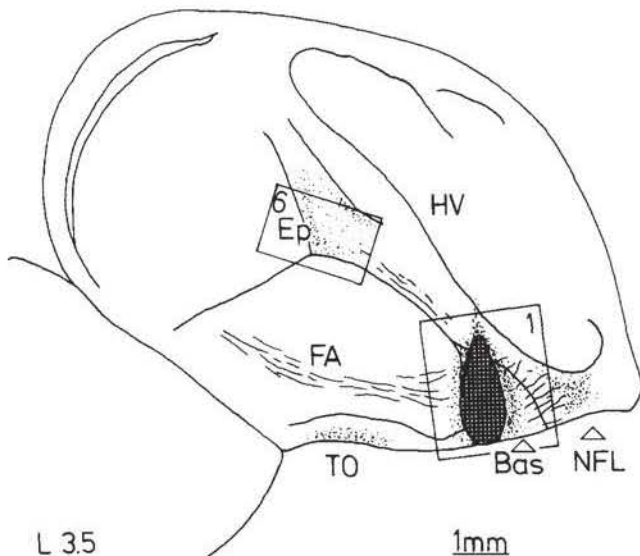




Figs. 1-5. All photomicrographs are from sagittal sections. Ventral is downward and frontal is to the right



**Fig. 6.** Photomicrograph of a sagittal section. Ventral is downward and frontal is to the right. Labeled fibres in the peri-ectostriatal belt following an HRP-injection into the Bas. The section corresponds to the L 3.00 plane according to the atlas of Karten and Hodos.  $\times 85$



**Fig. 7.** Intratellencephalic afferents of the Bas. The drawing of a sagittal section shows the injection site and the structures in which labelled neurons (*dots*) were found. The anterogradely labelled axons of the FA are shown to course through the Bas and the paleostriatum (*dashes*). Their terminal field in the archistriatum is more lateral than this section, which corresponds to the L 3.25 plane of the pigeon brain atlas (Karten and Hodos 1967)

starling, injections in the lateral part of the Bas yielded bilateral labelling of cells with a diameter of perikaryon of 8–15  $\mu\text{m}$  in the nucleus lemnisci lateralis, pars ventralis, a known auditory nucleus (LLv, Fig. 12). Since injections in medial parts of the Bas (L 2.50–L 3.50) yielded no HRP-positive neurones in the LLv it was concluded that the auditory input to the Bas is restricted to its lateral half. Fig. 13 shows the rhombencephalic afferents of the Bas.

#### Discussion

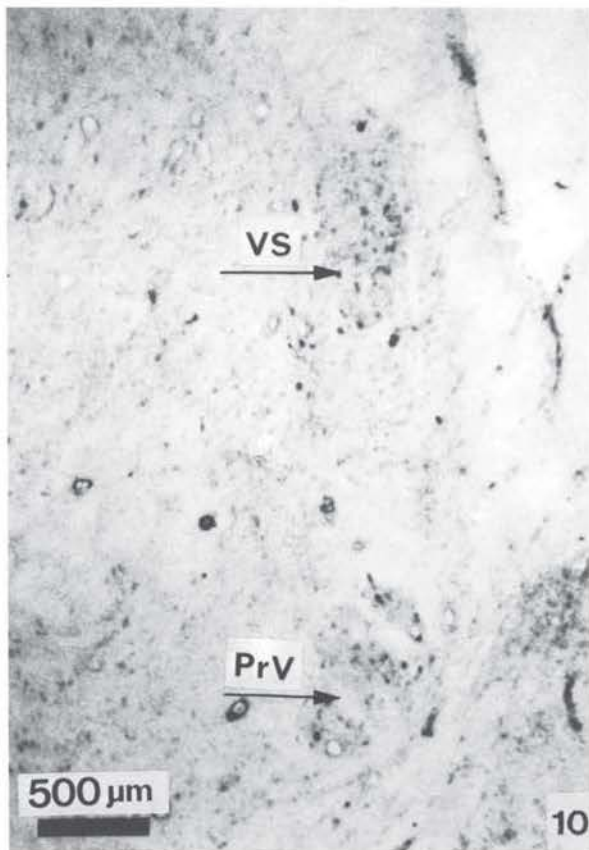
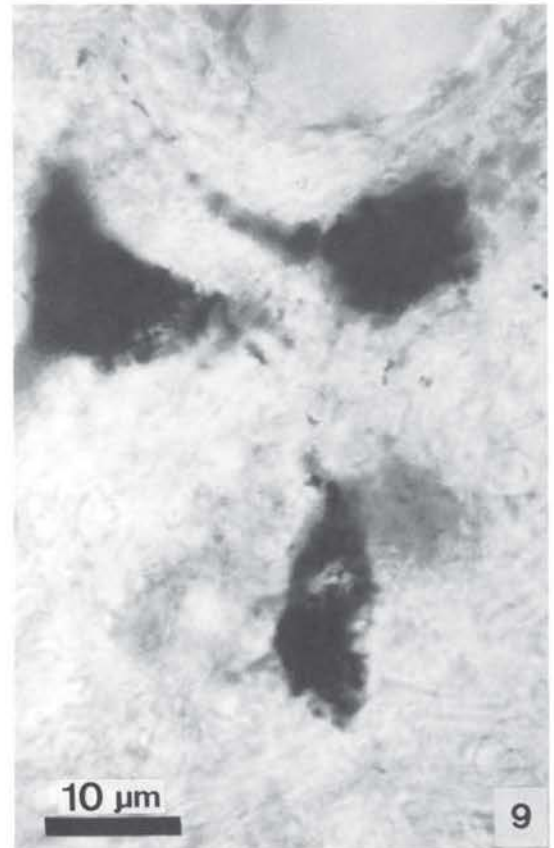
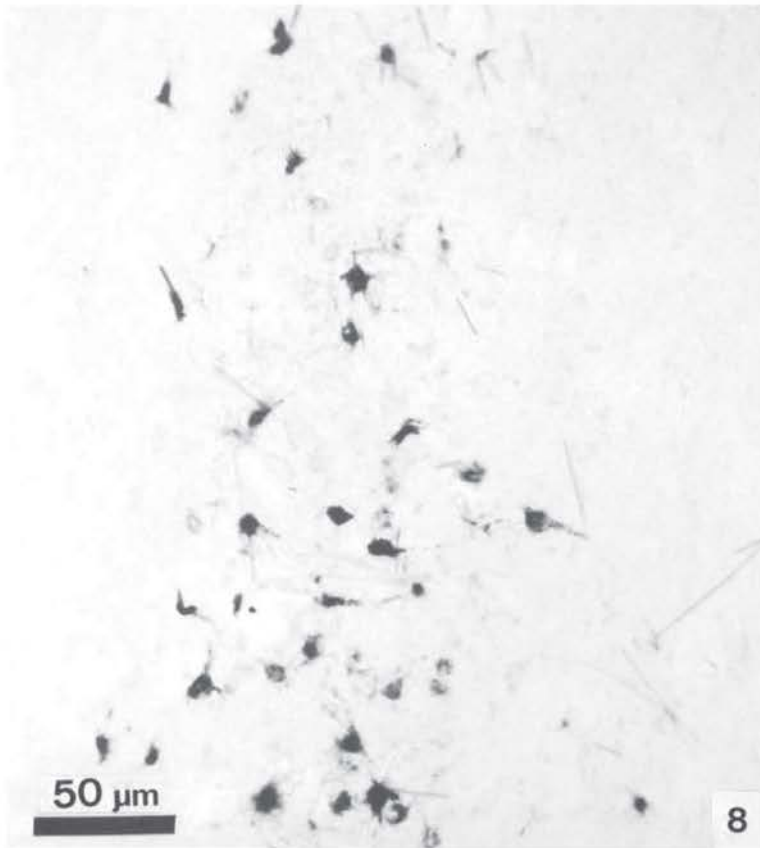
The results described above confirm several findings of previous anatomical and electrophysiological investigations concerning the sensory afferents to the nucleus basalis (Fig. 14). The projection of the PrV upon the Bas was demonstrated earlier by anterograde (Wallenberg 1903; Zeigler and Karten 1973; Dubbeldam et al. 1981; Wild et al. 1984) as well as by retrograde anatomical tract tracing methods (Kirsch 1983; Wild et al. 1984, 1985). The direct afferents of the Bas from the PrV are also confirmed by evoked potentials (Schall and Delius, in preparation) as well as by two studies with single-unit recordings (Witkovsky et al. 1973; Berkhoudt et al. 1981), which demonstrated that the neurones of the Bas can be activated with latencies of 3 ms by electrical and tactile stimulation of the beak. A bilat-

**Figs. 8–11.** Photomicrographs of sagittal sections. Ventral is downward and frontal is to the right

**Fig. 8.** Nucleus sensorius principalis nervi trigemini (PrV) with labelled fibres after HRP-injection into the Bas.  $\times 325$

**Fig. 9.** Enlargement of another section showing labelled neurones in the PrV.  $\times 1580$

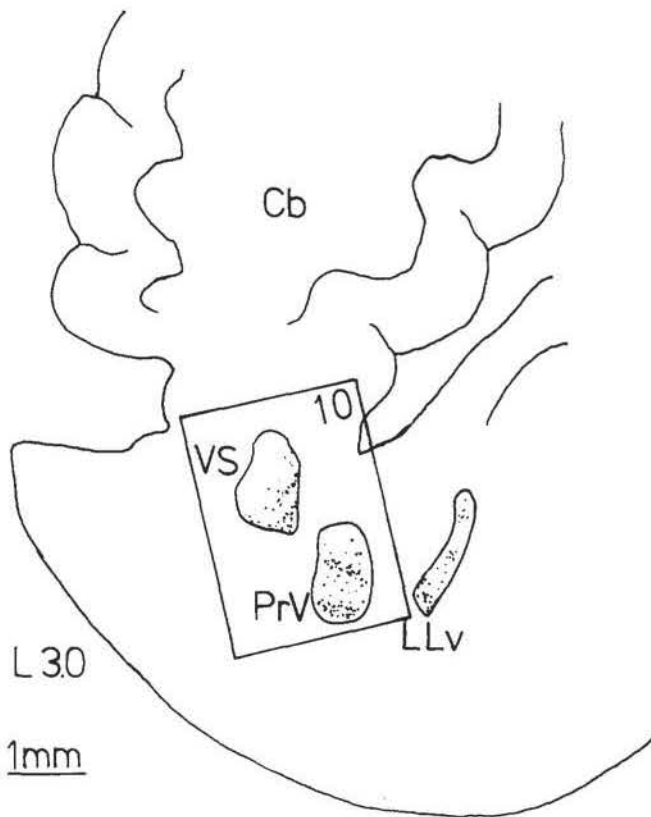




**Fig. 10.** Labelled neurones in the *PrV* and in the nucleus vestibularis superior (*VS*) after HRP injection into the Bas. The section corresponds to the L 3.00 plane of the atlas of Karten and Hodos.  $\times 26$

**Fig. 11.** Enlargement of Fig. 9 showing labelled neurones in the *VS*.  $\times 1020$

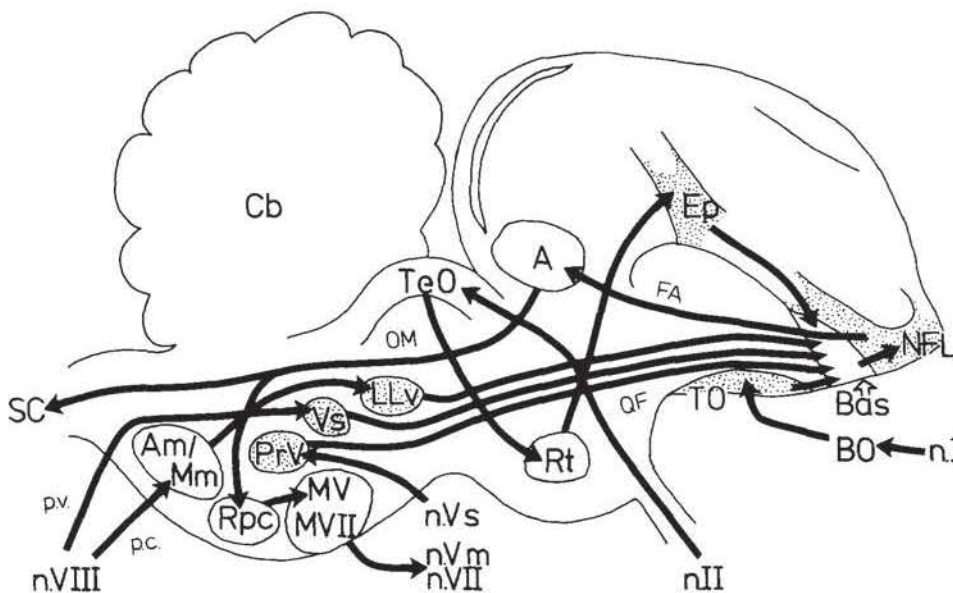
**Fig. 12.** Photomicrograph of a sagittal section. Labelled neurones in the nucleus lemnisci lateralis, pars ventralis (*LLv*) after an HRP-injection into the Bas.  $\times 500$



**Fig. 13.** Rhombencephalic afferents of the Bas. The drawing shows the structures in which labelled neurones (dots) were found. The section corresponds to the L 3.00 sagittal plane of the pigeon brain atlas (Karten and Hodos 1967)

eral projection from the LLv first described by Kirsch (1983) for the starling is now confirmed by our results for the pigeon. The LLv is known to receive direct input from the nucleus angularis, pars medialis and the nucleus magnocellularis, pars medialis, rhombencephalic terminations of the cochlear component of nerve VIII (Boord 1968; Correia et al. 1982). As in the case of the trigeminal somatosensory input to the Bas there are also electrophysiological data from single units (Berkhoudt et al. 1981; Kirsch 1983) and of evoked potentials with short latencies (Naumov and Iljitschev 1964; Harman and Phillips 1967; Delius et al. 1979; Schall and Delius, in preparation) which demonstrated that the neurones of the Bas can be activated by auditory stimulation.

Our findings, however, also show that the Bas receives further sensory inputs not thus far reported. Most striking is the direct crossed projection from the nucleus vestibularis superior (VS) indicating that the Bas should receive short latency input from the vestibular complex. The VS, a rhombencephalic termination of the vestibular component of nerve VIII, appears to receive input mainly from the ipsilateral ampullary receptors (Wilson and Fempel 1972; Wold 1975). Recent electrophysiological studies in cochlea-extirpated pigeons demonstrate that electrical stimulation of the contralateral canalis semicircularis caudalis (sagittal canal, Baumel 1979) leads to vestibularly evoked potentials of short latency (3.6 ms) in the Bas (Schall and Delius, in preparation), agreeing with a paucisynaptic pathway. Angular accelerations of the head lead to the activation of units in the Bas. It is remarkable that the somatosensory, auditory and vestibular pathways to a nucleus in the most anterior telencephalon, differing from the more orthodox avian tel-



**Fig. 14.** Afferents and efferents of the nucleus basalis prosencephali (Bas). Schematic diagram of a parasagittal section through the brain of a pigeon illustrating the main anatomical structures involved in the basalis circuit. The regions in which retrogradely labelled cell bodies were found after HRP-injections into the Bas in the present study are stippled.

*A* archistriatum, *Am* nucleus angularis, pars medialis, *BO* bulbus olfactorius, *Cb* cerebellum, *Ep* peri-ectostriatal belt, *FA* tractus fronto-archistriatalis, *LLv* nucleus lemnisci lateralis, pars ventralis, *Mm* nucleus magnocellularis, pars medialis, *MV* nucleus motorius nervi trigemini, *MVII* nucleus nervi facialis, *NFL* neostriatum frontolaterale, *n.I* nervus olfactorius, *n.II* nervus opticus, *n.Vm* nervus motorius trigemini, *n.Vs* nervus sensorius trigemini, *n.VII* nervus facialis, *n.VIII* nervus vestibulocochlearis, pars cochlearis (*p.c.*) et pars vestibularis (*p.v.*), *PrV* nucleus sensorius principalis nervi trigemini, *OM* tractus occipitomesencephalicus, *QF* tractus quintofrontalis, *Rpc* nucleus reticularis parvocellularis, *Rt* nucleus rotundus, *SC* spinal cord, *TeO* tectum opticum, *TO* tuberculum olfactorium, *VS* nucleus vestibularis superior.



encephalic sensory projections (Cohen and Karten 1974), all bypass thalamic relay stations. Wild et al. (1985) did not report any rhombencephalic afferents to the Bas other than from the PrV in their excellent study on the trigeminal system of the pigeon. But these authors made only an HRP injection into the Bas of a single pigeon in order to confirm the anterograde projection of the sensory trigeminal nucleus they had established. Afferents other than from the PrV might have been overlooked in this pigeon. That these afferents actually terminate in the Bas and where not labelled by the transport of interrupted fibres that pass through the Bas, is demonstrated by the electrophysiological data cited above and by the fact that the HRP-injection slightly rostral to the Bas did not result in a retrograde transport into any of the reported rhombencephalic or telencephalic sensory areas.

The present results also indicate that the Bas is likely to receive visual information since the HRP-injections in this structure yielded labelling of cell somata in the perieostriatal belt, a target of both the tectofugal (Karten and Hodos 1970) and the thalamofugal visual pathways (Ritchie and Cohen 1977). These anatomical data confirm electrophysiological results demonstrating that the neurones of the Bas respond to optic stimulation (Schall and Delius, in preparation).

The labelled cell bodies in the tuberculum olfactorium (TO) indicate that the Bas receives olfactory input from this structure. Although Rieke and Wenzel (1978) do not explicitly mention the TO in their study of the olfactory bulb projections in pigeons, it is apparent from their figures that they found degenerating terminals in the TO after olfactory bulb lesions. The electrophysiological evidence available (Macadar et al. 1980) is as yet unspecific about an olfactory projection to the Bas. The labelled neurones in the paleostriatum augmentatum were observed directly at the border to the Bas. Since we could not be certain that these neurones were not labelled by diffusion of HRP this result was not taken into consideration.

The spectrum of afferents to the Bas concur well with the conception that it is a sensorimotor coordinator for pecking (Zeigler 1976; Delius 1985). No special argument in this respect is required relating to the tactile input from the beak, as particularly the grasping/swallowing phase of a peck leading to the uptake of grains involves fine manipulative motions (Zweers 1982) that clearly are under the close control of local tactile feedback (Zeigler 1976). Concerning the auditory input to the Bas, although pigeons feed on silent food, pecks generate a good deal of noise as a result of impact and friction. This stimulus may support feedback that controls grasping and further pecking as we have explained elsewhere (Delius 1985). Bone conduction of peck-generated sound may be important. The jaw (beak) bones of birds are mechanically coupled with the tympanum and electrophysiological evidence suggests that sound conducted through the bones can activate the Bas (Schall and Delius, in preparation). The short latency, paucisynaptic transmission of tactile and auditory information seems essential if it is to have a feedback function since pecking in the pigeon is an exceedingly fast motion (Smith 1974; Zweers 1982).

Since pigeons close their eyes during the terminal phase of the pecking thrust as a protection against particle backscatter (Hodos et al. 1976; Delius 1985), it is understandable that visual information has a delayed, plurisynaptic access

to the Bas through the peri-ectostriatal belt as it cannot provide short-term feedback. However it most certainly could exercise feedforward control over pecking for which a longer latency would not be critical.

The probable olfactory input to the Bas does not disagree with functional considerations since such information is clearly useful for the quality control of food. That feeding in some bird species at least is indeed under the control of odours seems certain (Henton 1969; Würdinger 1979). One is left to wonder about a gustatory input to the Bas as much the same can be said for the role of taste in feeding (Gentle 1975; Marriotti and Fiore 1980). This needs further investigation.

The fact that the final pecking thrust of pigeons is visually ballistic makes it almost mandatory that the considerable accelerations of the head during this movement phase should be under fast vestibular feedback control. Having provided evidence that the neural circuitry for such reafferents is present in the pigeon is the most important result of our study.

The three ascending sensory projections to the Bas all bypass the thalamus to terminate directly in the telencephalon. This makes the Bas an unusual structure, which is probably unique to birds. Since this organisational pattern challenges the concept of a 'Bauplan' common to all vertebrate brains, Cohen and Karten (1974) suggested that the Bas is actually a displaced thalamic nucleus and that the neighbouring NFL is in fact the primary telencephalic trigeminal projection area. This interpretation conforms with the parcellation theory of the evolution of the vertebrate brain, which would posit that the avian rhombencephalic auditory, vestibular and trigeminal nuclei could not bypass the thalamus to invade the telencephalon (Ebbesson 1984). However, ontogenetic studies have not so far produced evidence that would support the highly speculative hypothesis that the Bas is a thalamic nucleus (Källen 1962). It seems thus more reasonable to accept the Bas for what it is: a telencephalic structure with sensory afferents from rhombencephalic nuclei.

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