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A pathway for predation in the brain of the barn owl (*Tyto alba)*:

projections of the gracile nucleus to the 'claw area' of the rostral Wulst, via the dorsal thalamus

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Abstract

The Wulst of birds, which is generally considered homologous with the isocortex of mammals, comprises an elevation on the dorsum of the telencephalon that is particularly prominent in predatory species, especially those with large, frontally placed eyes, such as owls. The Wulst, therefore, is largely visual, but a relatively small rostral portion is somatosensory in nature. In barn owls this rostral somatosensory part of the Wulst forms a unique physical protuberance dedicated to the representation of the contralateral claw. Here we investigate whether the input to this 'claw area' arises from dorsal thalamic neurons that, in turn, receive their somatosensory input from the gracile nucleus. Following injections of biotinylated dextran amine into the gracile nucleus and cholera toxin B-chain into the claw area, terminations from the former and retrogradely labeled neurons from the latter overlapped substantially in the thalamic nucleus dorsalis intermedius ventralis anterior. These results indicate the existence in this species of a 'classical' trisynaptic somatosensory pathway from the body periphery to the telencephalic Wulst, via the dorsal thalamus, one that is likely involved in the barn owl's predatory behavior. The results are discussed in the context of somatosensory projections, primarily in this and other avian species.

Keywords

Somatosensory; evolution; thalamus; owl; Wulst

INTRODUCTION

In the few avian species thus far investigated there is a classical three-neuron somatosensory projection system from the body periphery (as distinct from the beak; see below) to the forebrain, via synapses in the dorsal column nuclei (DCN: gracile and cuneate nuclei), dorsal thalamus and rostral Wulst (Wild, 1985; 1987a; 1989; 1997; Funke 1989a; 1989b). The avian Wulst - which is generally considered homologous with the isocortex of mammals - comprises an elevation on the dorsum of the telencephalon that is especially massive in species with frontally placed eyes, such as the barn owl (Karten et al., 1973). Thus, the Wulst is largely a visual structure, but it has a relatively small rostral component that is somatosensory in nature (Karten et al., 1978; Manger et al., 2002; Wild, 1987a; Funke, 1989a). In barn owls, this somatosensory part of the Wulst forms a specialized protuberance at the rostral pole of the telencephalon, immediately dorsal to the olfactory lobes (Fig. 1). It

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Corresponding author: J Martin Wild, Phone (+64) (9) 373-7599 Ext 86054, Fax (+64) (9) 3737484, Email jm.wild@auckland.ac.nz contains complete, dual mirror image representations of the contralateral claw, particularly its plantar, grasping surface (Manger et al., 2002). This surface, which is covered by tactile tubercles, seems ideally suited to the bird's natural predatory behavior, in which the claws lead the strike and hold the prey before tearing with the beak. On the basis of retrograde tracing, the rostral Wulst receives a projection from a nucleus in the dorsal thalamus known as dorsalis intermedius ventralis anterior (DIVA; Karten et al., 1978), but since the ascending projections to DIVA were never investigated, it is not known whether barn owls, like other birds, possess a classical three-neuron somatosensory projection, with relays in the dorsal column nuclei and dorsal thalamus.

The main purpose of the present study, therefore, was to investigate the possibility of such a pathway. This is of comparative interest, particularly in the context of other somatosensory projections from the body and beak that reach other regions of the telencephalon in birds, including barn owls, both trisynaptically and disynaptically (Wild, 1987a; 1997; 1994; Funke, 1989b; Schneider and Necker, 1989; Wild et al., 1997; 2001).

Contrary to frequently held assumptions about the (lack of) organization of the DCN in birds (see Wild, 1985), the barn owl's gracile and cuneate nuclei can be clearly distinguished, facilitating the tracing of their projections individually. On the basis of retrograde tracing studies, both gracile and cuneate nuclei in this species appear to project upon a large nucleus in the lateral pons, called pontis externus (PE) (Wild et al., 2001). PE then projects massively upon nucleus basorostralis (Bas) in the anterior part of the pallium, a nucleus that in all avian species is the recipient of a major trigeminal projection that conveys sensory input disynaptically from the beak and oral cavity, via the principal sensory nucleus (Wallenburg, 1903; Dubbeldam et al., 1981; Wild et al., 1985; 2001; Wild and Farabaugh, 1996). In Bas of barn owls and budgerigars, there is a complete representation of the whole body, including claws, legs, body, wing, beak, tongue, and even the cochlea, the last one being mediated via the intermediate nucleus of the lateral lemniscus, as in pigeons (Arends and Zeigler, 1986; Wild et al., 1997; 2001). In the barn owl, however, the ascending projections from DCN to PE and the dorsal thalamus were not investigated anterogradely, so a likely input to DIVA remained undetermined.

MATERIALS AND METHODS

Data were obtained from four female and one male adult barn owls (*Tyto alba*) bred in captivity at the California Institute of Technology. Each was anesthetized by an intramuscular injection of ketamine hydrochloride (50 mg/kg Ketaject, Phoenix Pharmaceuticals, Mountain View, CA) and xylazine (20 mg/kg XylaJect, Phoenix Pharmaceuticals, Mountain View, CA), wrapped in a leather jacket, and held in fixed position in a custom-made stereotaxic frame with ear bars and a beak holder. Supplementary injections of ketamine and xylazine mixture were given as required to maintain surgical anesthesia. Craniotomies were made over the caudal cerebellum and/or the contralateral rostral Wulst for recording and injection, packed with gelfoam and sealed with dental cement at the end of the session, and the scalp sutured. After surgery, analgesics (Ketoprofen, 10 mg/kg, Ketofen, Merial USA, www.us.merial.com) were administered intramuscularly and the animals were returned to their cages after complete recovery from anesthesia. The protocol for this study followed the National Institutes of Health Guide for the Care and Use of Laboratory Animals and was approved by the Institute's Animal Care and Use Committee.

For injections in the rostral Wulst (Fig. 2), the beak was raised to provide ease of access to the frontal pole of the brain. For injections in the gracile nucleus (Figs. 3A and 3B), the head was held with the beak pointing down with respect to the horizontal position. To locate and define the relevant structures physiologically a tungsten microelectrode (3-4 MΩ) was lowered either directly into the rostral protuberance of the Wulst under direct visual guidance, or through the depth of the cerebellum to reach the DCN. Multiunit activity evoked by tactile stimulation of the contralateral claw (to identify the rostral Wulst) or of the ipsilateral claw (to locate the gracile nucleus) was recorded oscillographically and over a loud speaker following appropriate signal filtering and amplification. Tactile stimuli were applied either by brief (0.5 ms) indentations of the keratinised epithelium by a sharp wooden probe attached to the membrane of a loudspeaker and pulsed by a Grass stimulator, or by gentle squeezing and stroking of the foot or of individual digits of the claw. Robust phasic and tonic responses to these stimuli could be recorded from the contralateral rostral Wulst and, with much shorter latencies, from what was assumed to be the gracile nucleus located ~ 0.5-1 mm from the midline in the caudal medulla. This evoked unit activity was used to guide glass micropipettes to the recording site following the search with the tungsten microelectrode. For injections in the rostral Wulst the pipette (internal diameter of tip ~ 20μ) was loaded with 1% cholera toxin B subunit (List Biological Laboratories, Campbell, CA) in PBS. For injections in the gracile nucleus, the pipette was loaded with 10% biotinylated dextran amine (BDA, 10K MW; Invitrogen, Eugene, OR) in phosphate buffered saline (PBS), pH7.4. Multiunit responses to tactile stimuli applied to the claw were re-recorded through the pipette to locate the appropriate depth in the rostral Wulst (IHA: interstitial hyperpallium apicale, the principal thalamorecipient layer of the Wulst; Fig 2A) and to substantiate placement in the gracile nucleus. A wire in contact with the solutions in the pipette allowed positive current (2-4 μA) to be applied from a high voltage current source intermittently for 20-30 minutes (iontophoresis) to deposit the tracer.

Following a 4-7 day survival time, the birds were deeply anesthetized and perfused through the heart with 0.9% saline followed by 4% paraformaldehyde in phosphate buffer, pH 7.4. The brains were extracted from the skull, postfixed overnight, blocked in a coronal plane and equilibrated in 30% sucrose buffer. When the brains had sunk, they were sectioned on a freezing microtome at 50μ and collected in PBS in 4 columns and 6 rows. Different rows were treated so as to reveal either BDA alone, CTB alone, or BDA and CTB together in the same sections. All sections were preincubated in 3% H_2O_2 in 1:1 PBS:butanol for 10 mins to block the activity of endogenous peroxidase and all treatments were separated by 3 × 10 min washes in PBS. BDA was visualized using streptavidin peroxidase conjugate (Invitrogen, Eugene, OR) at 1:1,000 dilution plus 0.4% Triton X-100 in PBS for 1 hour, followed by a reaction in diamino benzidine (0.025%), H_2O_2 and 0.02% cobalt chloride to yield a black reaction product. CTB was visualized using an anti-CTB antibody raised in goat (List Biological Laboratories, Campbell, CA) at 1:33,000 dilution plus 3% normal rabbit serum in Triton X-100 in PBS for 15 hours, followed by incubation in a biotinylated anti-goat secondary antibody raised in rabbit (1:200 for 1 hour; Sigma-Aldrich.com) and finally streptavidin peroxidase conjugate for a further 1 hour. The reaction product was also colored black using 0.02% cobalt chloride, as for BDA. When both BDA and CTB were visualized in the same sections, however, the above procedures were carried out sequentially, such that BDA was visualized first and colored black, and CTB second, with cobalt chloride omitted from the DAB mixture, so as to yield a brown reaction product. Thus, the black BDA anterograde labeling resulting from injections in the gracile nucleus could be distinguished from, and visualized in proximity to, brown retrogradely labeled cell bodies resulting from injections of CTB into the rostral Wulst. Sections were mounted on subbed slides and coverslipped with DePeX. The material was photographed using a Kontron ProgRes 3008 digital camera attached to a Leica DMRA microscope, and captured using Adobe Photoshop with the appropriate plug-in. The images were processed with Adobe PhotoShop v.5.5 software to produce the final figures.

RESULTS

Ascending projections from the DCN injections

Since the injections of BDA in the gracile nucleus (G) were made on the basis of its electrophysiological identification, they were centered upon it, although there was some involvement of adjacent structures, including the cuneate nucleus laterally and medial parts of the trigeminal dorsal horn and possibly the nucleus of the solitary tract ventrally (Figs. 3A and 3B). There was no involvement of cochlear or vestibular nuclei. These injections resulted in labeled axonal tracts and terminal fields throughout the brainstem and thalamus, predominantly contralaterally. Proceeding rostrally from the level of the injection, a distinct terminal field was found in the lateral portion of the ventral lamella of the inferior olive (OIv) (Figs. 3A and 3C). At rostral pontine levels, a circumscribed terminal field consisting of densely labeled, swirl-like structures was seen in the contralateral nucleus pontis externus (PE: Figs. 3D and 3E), a large, kidney shaped nucleus that makes a distinct bulge on the lateral aspect of the pons at the level of the caudal pole of the anterior part of the dorsal nucleus of the lateral lemniscus. PE was originally identified on the basis of its ascending projections to Bas and its retrograde labeling of DCN (Wild et al., 2001). A distinct projection from G was also seen to the outer aspect of the inferior colliculus (IC, *aka* MLd, torus semicircularis: Figs. 4A and 4C), with fibers and terminations sparsely distributed throughout the center of the nucleus itself (arrows in Fig. 4C). The terminal field on the outer aspect of IC consisted of a relatively dense part over the superficial part of the nucleus (ICS) and a sparser region covering its dorsal lip (ICX) and the perimeter of the medial and lateral shells. The rostromedial pole of IC, which bulges into the fourth ventricle at these levels, was entirely occupied by fibers and terminations (Fig. 4B and 4D). (Note, the coronal angle used here is slightly different from that of Knudsen (1983) and of Wagner et al. (2003), resembling more that of Levin et al. (1997)). Unlike observations in pigeons (Wild, 1995), no DCN projections to somatosensory nuclei located ventral to IC were found. At the level of the mesencephalic-diencephalic junction there was a small, ventrally located, but unidentified terminal field (Fig. 4B) and a diffuse field of fibers and terminations ventral to the medial spiriform nucleus (not shown). Finally, a discrete, vertically oriented terminal field was found on the lateral aspect of the dorsal thalamus, immediately dorsal to the dorsal tip of the massive principal optic nucleus (OPT; Fig. 5; and see below). This projection, which was entirely contralateral, extended caudorostrally from the level of nucleus ovoidalis (Ov; the proposed homolog of the ventral nucleus of the medial geniculate body of mammals) to the level of the dorsal part of the superior reticular thalamic nucleus (RSd). No other projections to the dorsal thalamus were observed. Ipsilaterally, a small projection was observed to medial aspects of the principal sensory trigeminal nucleus (not shown), but no projections were found to other parts of the trigeminal brainstem nuclear complex or to parabrachial nuclei.

Retrogradely labeled neurons resulting from Wulst injections

A CTB injection in the protuberance of the rostral Wulst and the resulting retrogradely labeled cells in proximity are shown in figure 2B. A separate, conspicuous cluster of labeled cells was also found more dorsally and laterally at rostral levels (Fig. 2A). Counterstained sections revealed that these neurons lay within the mesopallium. No other retrogradely labeled cells were found in the telencephalon, but a distinctive cluster was found in the thalamus, immediately dorsal to OPT (Fig. 5). These cells, largely, but not entirely, ipsilateral to the rostral Wulst injection, we suggest form the most lateral part of DIVA, a nucleus originally defined by Karten et al. (1978) in the burrowing owl and subsequently extended to other species such as pigeons and finches (Wild, 1987a; 1997; Funke, 1989a; see below and Discussion).

No descending projections from the rostral Wulst upon the thalamus were observed.

Figure 5 shows anterograde and retrograde labeling in DIVA resulting from an injection of BDA in the gracile nucleus and another of CTB into the contralateral rostral Wulst in the same bird. The black BDA fiber and terminal labeling and the brown retrogradely labeled cell bodies can be seen to overlap substantially in the lateral part of DIVA, indicating a specific projection from neurons at the site of injection in the DCN to DIVA neurons that project to the claw area of the rostral Wulst. Some relatively sparse fiber and terminal labeling extended medially from the region of overlap with retrogradely labeled cells towards what we suggest are more medial parts of DIVA located dorsal to RSd. It is this medial cell group, rather than the more lateral neurons in the overlap region, that has been designated DIVA in pigeons and finches (Wild, 1987a;1989;Funke, 1989a) - see Discussion.

DISCUSSION

The principal aim of this study was to determine whether the barn owl possesses a trisynaptic somatosensory projection from the body periphery - in this case the claw - to the claw area of the rostral Wulst, via relays in the gracile nucleus and dorsal thalamus. Despite the lack of retrograde confirmation that the gracile nucleus specifically provides the ascending projection to DIVA, we believe that this aim was very largely achieved. This belief is based on the following considerations: (1) The gracile nucleus in the barn owl can be clearly distinguished from the adjacent cuneate nucleus in normal material and has been additionally defined on the basis of its receipt of projections from the sciatic nerve (Wild et al., 2001). It has a larger cross-sectional area than the cuneate nucleus, at least at caudal levels, perhaps indicating its functional importance in the life of the bird. (2) The injections aimed at the gracile nucleus made in the present study were electrophysiologically guided and the resulting deposits of BDA were centered on the nucleus, although there was some diffusion of tracer laterally to include part of the cuneate nucleus and ventrally to include a medial part of the trigeminal dorsal horn. (3) The major terminal field within the contralateral dorsal thalamus resulting from injections centered on the gracile nucleus was very largely in register with neurons retrogradely labeled from the physiologically defined ‘claw area’ of the rostral Wulst (the overlap region), indicating a specific projection from the gracile nucleus. The ‘claw area’ of the rostral Wulst does not appear to contain the representation of any body parts other than the claw, foot and perhaps leg (Manger et al., 2002; see below). However, a small number of BDA-labeled fibers and terminal labeling extended medially from the overlap region in the dorsal thalamus, but whether this resulted from uptake by neurons outside the gracile nucleus (e.g., the cuneate nucleus), or whether the extent of the retrograde labeling was the result of a sub-total injection in the claw area, is not known. It should be noted, however, that although Manger et al. (2002) speculated that the rostral Wulst in the barn owl might contain a full body representation, they did not find other than claw, foot, and a few leg units. They also noted that, even if the rostral Wulst did contain a full body representation, the representation of body parts other than the claw would necessarily be very small due to the huge representation of the claw itself. This suggests that the neurons retrogradely labeled from the injections in the rostral Wulst mediate input very largely from the claw; indeed, most of these neurons were overlapped by fibers and terminations resulting from the injections centered on the gracile nucleus. Nevertheless, it seems likely that the cuneate nucleus, as well as other parts of the DCN that receive body input, do project to the dorsal thalamus, as they do in other birds (e.g., pigeons and finches: Wild, 1987a; 1989; 1997), but whether they project topographically to more medial parts of DIVA, e.g., to that part of the nucleus located dorsal to RSd and FPL, and whether the recipient neurons then project to the rostral Wulst or to some other part of the telencephalon, remains to be determined. In other species such as pigeons and finches that do not possess the somatosensory protuberance of the barn owl, the whole body (minus the beak) is nevertheless represented in a rostral part of the Wulst (Wild, 1987a; 1997; Funke, 1989a). (4) The projections throughout the brainstem and thalamus resulting from the injections centered on the gracile nucleus are largely consistent with those of the DCN as described in other avian species (Wild, 1987a; 1989; 1995; 1997; Funke, 1989b) and are generally inconsistent with those described for either the spinal trigeminal or solitary tract nuclei (Arends et al., 1984; 1988). The exception was a small ipsilateral projection to the medial aspect of the principal sensory trigeminal nucleus, which may have arisen from ventral spread from the injection site to medial aspects of the trigeminal dorsal horn. Such ipsilateral intertrigeminal projections have been described in the mallard (Arends et al., 1984). Thus far, no evidence exists from orthograde tracing studies for a trigeminal projection to the dorsal thalamus in birds (Arends et al., 1984), although retrograde tracing and electrophysiological studies have suggested that there might be a small projection to caudal thalamic regions, but not to DIVA (Delius and Bennetto, 1972; Witkovsky et al., 1973; Korzeniewska, 1987; Schneider and Necker, 1989; Korzeniewska and Güntükün, 1990). (6) Although DIVA in barn owls might receive a spinothalamic projection, as DIVA does from the lumbar cord in pigeons (Schneider and Necker, 1989), the trajectory of spinothalamic fibers through the medulla does not include the DCN. Therefore, the observed projections seem unlikely to be accounted for by uptake of tracer by spinothalamic fibers of passage at the site of injection.

Although ascending projections of the gracile nucleus to the dorsal thalamus were the main focus of the present study, other projections are briefly discussed here (a) because they help validate the projections of specific interest, (b) for comparative interest and (c) for the sake of completion. The projection to the inferior olive confirms similar findings in other avian species: mallard (Arends et al., 1984), pigeon (Wild, 1989), finch (Wild, 1997), and likely provides a means whereby somatosensory information can reach the cerebellum, there being no reported direct projection from the DCN to the cerebellum in birds.

The projection to PE confirms our previous findings in barn owls made on the basis of retrograde labeling resulting from injections of CTB into PE (Wild et al., 2001). Such injections also retrogradely labeled cells in the cuneate nucleus, suggesting that PE probably contains a representation of the whole body, which is then re-represented in Bas, to which PE massively projects. The claw, therefore, is represented at least twice in the barn owl brain, once in the rostral Wulst and another in Bas, the latter along with the leg and the rest of the body (cf Manger et al., 2002).

Because injections of retrograde tracer were not made in the midbrain in the present study, it cannot be concluded that the projections thereto arise specifically from the gracile nucleus. However, the same considerations mentioned above regarding the probability of gracile projections to DIVA apply in this situation also. For instance, there are no known projections from either trigeminal or solitary tract nuclei to the torus semicircularis in birds (Arends et al., 1984; 1988). Moreover, the projections observed in the present study are consistent with somatosensory projections from the DCN to the midbrain as defined in pigeons and finches on the basis of both anterograde and retrograde tracing studies (Leibler, 1975; Wild, 1989; 1995; 1997). In pigeons, not only are there specific DCN projections to what appear to be dedicated somatosensory nuclei of the mesencephalon (Ballam, 1982; Leibler, 1975; Wild, 1995), but also to parts of the auditory torus itself, including its central nucleus, as found in the barn owl in the present study (Wild, 1995). This apparent overlap of somatosensory and auditory projections within parts of the IC is especially noteworthy in the barn owl, in which the putative projections from the gracile nucleus are quite prominent to the outer periphery of rostodorsal parts of the nucleus. Although speculative, it may be that this region of the IC is particularly sensitive to low frequency sounds (Wagner, personal communication), which might be on a continuum with signals transmitted via the sciatic nerve from receptors located between the leg bones that sense vibrations in the substrate (Dorward and McIntyre, 1971). In contrast, projections from the dorsal column nuclei to nuclei located immediately ventral to more caudal levels of the IC that have been described in pigeons and finches (Wild, 1995; Wild, 1997) were not found in the present study in the barn owl. The subsequent projections of midbrain regions receiving somatosensory projections have not been worked out in detail, although they may involve regions in proximity to the auditory thalamic nucleus ovoidalis, as shown by Wild and Williams (2000).

Comparative considerations

Ascending projections—Avian somatosensory projections are curiously and interestingly variable in different orders (Fig. 6). However, one thing common to all of them thus far investigated, including the barn owl (present study), is a classical three-neuron projection system involving a primary sensory neuron innervating some part of the body below the head, a secondary sensory neuron in the DCN, and at least one other sensory neuron in the dorsal thalamus. This basic vertebrate pattern can be found in teleost fish, amphibians, reptiles and mammals (e.g., Ito et al., 1986; Berkley et al., 1986; Muñoz et al., 1995;1997;Finger, 2000). In birds, as in several other vertebrates, there is frequently more than one dorsal thalamic nucleus receiving projections from the dorsal column nuclei. In pigeons and finches there is not only a DIVA, as in barn owls, but also a more caudal thalamic nucleus, called DLPc in pigeons (Wild, 1987a;Wild, 1989) or Uva in songbirds (Wild, 1994). DLPc/Uva has its terminal field within the dorsal ventricular ridge of the telencephalon, separate from that of DIVA in the rostral Wulst, but, like the rostral Wulst, not including a trigeminal component (Funke, 1989b;Wild, 1987a). Barn owls appear to lack a projection from the gracile nucleus to a thalamic nucleus more caudally situated than DIVA (present study); and, as mentioned above, it is not known whether the cuneate nucleus also projects to DIVA and/or to other parts of the thalamus. Parakeets might have a DCN projection to the dorsal thalamus, but this awaits demonstration.

In three of the groups shown in figure 6, there is a most curious primary afferent projection from the body (as indicted by projections of the sciatic and radial nerves) directly to a region immediately ventral or ventrolateral to the principal sensory trigeminal nucleus (PrV) and/or to parts of PrV itself. As far as we are aware, primary afferent projections from the body that extend as far rostrally as this within the brainstem have not been found in any other vertebrate class. In pigeons this projection is very sparse and diffuse, terminating within PrV and its surrounds (Wild, 1985); in budgerigars the projection terminates as a distinct terminal field in a nucleus immediately ventral to PrV called the subprincipal nucleus (sP; Wild et al., 1997); and in barn owls the projection terminates within PrV and in the caudal part of the intermediate nucleus of the lateral lemniscus (LLIc; Wild et al., 2001), otherwise known as nucleus paraprincipalis lateralis (Takahashi and Konishi, 1988). Since the trigeminal nerve, which innervates the beak of all birds, is topographically represented in PrV (Dubbeldam and Karten 1978;Dubbeldam, 1980;Wild and Zeigler, 1996), this means that the whole body is somatotopically represented in a distorted ‘homuncular’ fashion at pontine levels in these species, and again within Bas, to which PrV, sP and LLIc all project (Arends and Zeigler, 1986;Wild et al., 1985;1997;2001). In pigeons and finches, the representation of the beak is separate from that of the rest of the body, the beak being represented in Bas and the body in the rostral Wulst (Funke, 1989a;Wild, 1987a;Wild, 1997;Wild and Farabaugh, 1996). In barn owls somatosensory projections from the body reach Bas not only via LLIc but also, much more robustly, via PE. This particular route of somatosensory projections has not been noted in any other species.

As in birds and mammals, a projection to the torus semicircularis mediated by the medial lemniscus and originating from the DCN or one of its funicular nuclear homologs has been described in a teleost (Finger, 2000) and in amphibians (Muñoz et al., 1995). In fish and amphibians, auditory (octaval), mechanosensory and electrosensory inputs to the torus have traditionally been described as terminating separately (Bell, 1981; McCormick, 1982; 1989; De Wolf et al., 1983; Haugede-Carre, 1983; Echteler, 1984; Finger and Tong, 1984; Boord and Northcutt, 1988), but in birds, reptiles and lamprey there seems to be some overlap of auditory and somatosensory inputs to the torus (Belekhova et al., 1985; Künzle, 1986 Wild, 1995; present study; Gonzáles et al., 1999).

As outlined above and demonstrated in figure 6, birds, unlike mammals, have one or more parts of the somatosensory and auditory projection systems that bypass the thalamus altogether, thereby providing disynaptic projections from the periphery to the telencephalon. These systems should not be regarded as aberrant evolutionary solutions to the problem solved in mammals by the thalamocortical projection system. Rather they signify a radically different organization of major sensory systems, which in birds (and possibly in reptiles: Sieman and Künzle, 1994a;b) are comprised of both a thalamic bypass system as well as a dorsal thalamic system for telencephalic sensory representation. Moreover, the tendency of projection systems to bypass what have traditionally been considered obligatory relay nuclei is limited neither to the thalamus nor to the somatosensory system, as already shown in this and previous studies. Thus, in summary, in the somatosensory system of birds, primary afferent neurons in the dorsal root ganglia project not only to the spinal cord and DCN, as in other vertebrate classes, but also to paraprincipal regions in the pons, which then project directly to Bas in the telencephalon. In addition, the DCN project not only to the midbrain and dorsal thalamus, as in other classes, but, at least in barn owls, also to a lateral pontine nucleus (PE), which then projects directly to Bas. Similarly in the auditory system, two lateral lemniscal nuclei, LLD and LLV, project, in addition to the auditory midbrain, directly to Ov in the dorsal thalamus (Wild, 1987b), thereby bypassing the midbrain entirely; and paraprincipal and other lateral lemniscal nuclei (LLIc and LLIr) project directly to Bas, also bypassing the thalamus (Arends and Zeigler, 1986;Wild and Farabaugh, 1996;Wild et al., 1997;2001). It therefore seems that birds in particular, and possibly sauroposids in general, have evolved - or retained - a dual mode of telencephalic sensory representation at least for the somatosensory and auditory projections, one involving the dorsal thalamus and one that bypasses it. Mammals, on the other hand, appear to have opted, for the most part, for a single mode of telencephalic sensory representation involving the dorsal thalamus, albeit one with multiple submodality projection subsystems.

Descending projections—No projections upon DIVA were observed as resulting from injections of CTB into the claw area of the rostral Wulst in the barn owl, but since these injections were made at loci from which somatosensory responses could best be evoked by claw stimulation, they were centered on the deeper thalamorecipient layer IHA, rather than the more superficial layer HA (Manger et al., 2002), which supplies the efferent projections from the Wulst (Reiner and Karten, 1983; Miceli et al., 1987; Wild and Williams, 1999; 2000). Projections from the visual Wulst of owls and pigeons terminate within the principal optic nuclei of the thalamus, partly upon the neurons of origin of the projections to the Wulst (Karten et al., 1973; Miceli et al., 1979; 1987; Bravo and Pettigrew, 1981). In pigeons, a sparse projection from HA of the somatosensory Wulst to DIVA was reported by Wild and Williams (2000). These observations render untrue the oft-stated ‘fact’ that birds differ from mammals in lacking reciprocal cortico-thalamic connections. Furthermore, a closer and more directed search for such connections in birds may reveal not only their more general presence, but an organization similar to that in mammals, in which cortico-thalamic projections arise from a different layer than those which receive the thalamo-cortical projections.

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ABBREVIATIONS

Bas, basalis	Nucleus basorostralis
C	Nucleus cuneatus
Cbd	Tractus spinocerebellaris dorsalis
cc	central canal
CP	Commissura posterior
DCN	Dorsal column nuclei
DIVA	Nucleus dorsalis intermedius ventralis anterior
DLM	Nucleus dorsolateralis anterior thalami, pars medialis
DMNX	Dorsal motor nucleus of the vagus nerve
DS	Supraoptic ducussation
FLM	Fasciculus longitudinalis medialis
FPL	Fasciculus prosencephali lateralis
G	Nucleus gracilis
GCt	Substantia grisea centralis
HA	Hyperpallium apicale
IC	Inferior colliculus
ICo	Nucleus intercollicularis
ICS	Superficial inferior colliculus
ICX	External nucleus of the inferior colliculus
IHA	Interstitial hyperpallium apicale
IVv	Fourth ventricle
LLD	Dorsal nucleus of the lateral lemniscus
LLDa	Dorsal nucleus of the lateral lemniscus, anterior part
LLIc	Intermediate nucleus of the lateral lemniscus, caudal part
LLIr	Intermediate nucleus of the lateral lemniscus, rostral part
LLV	Ventral nucleus of the lateral lemniscus
M	Mesopallium
MLd	Nucleus mesencephalicus lateralis, pars dorsalis
N	Nidopallium
NI/NC	Nidopallium intermedium and caudale
NIf	Nucleus interface

NL	Nucleus laminaris
nTTD	Nucleus et tractus descendens nervi trigemini
OId	Nucleus olivarus inferior (dorsal lamella)
OIv	Nucleus olivarus inferior (ventral lamella)
OM	Tractus occipitomesencephalicus
OPT	Principal optic nuclei of the thalamus.
Ov	Nucleus ovoidalis
PE	Nucleus pontis externus
PrV	Nucleus sensorius principalis nervi trigemini
RPgc	Nucleus reticularis pontis caudalis, pars gigantocellularis
RSd	Nucleus reticularis superior, pars dorsalis
Ru	Nucleus ruber
sP	Subprincipal nucleus
SpM	Nucleus spiriform medialis
SSp	Nucleus supraspinalis
TeO	Tectum opticum
Uva	Nucleus uvaeformis
v	ventricle
XIIts	Nucleus tracheosyringealis (of CN XII)

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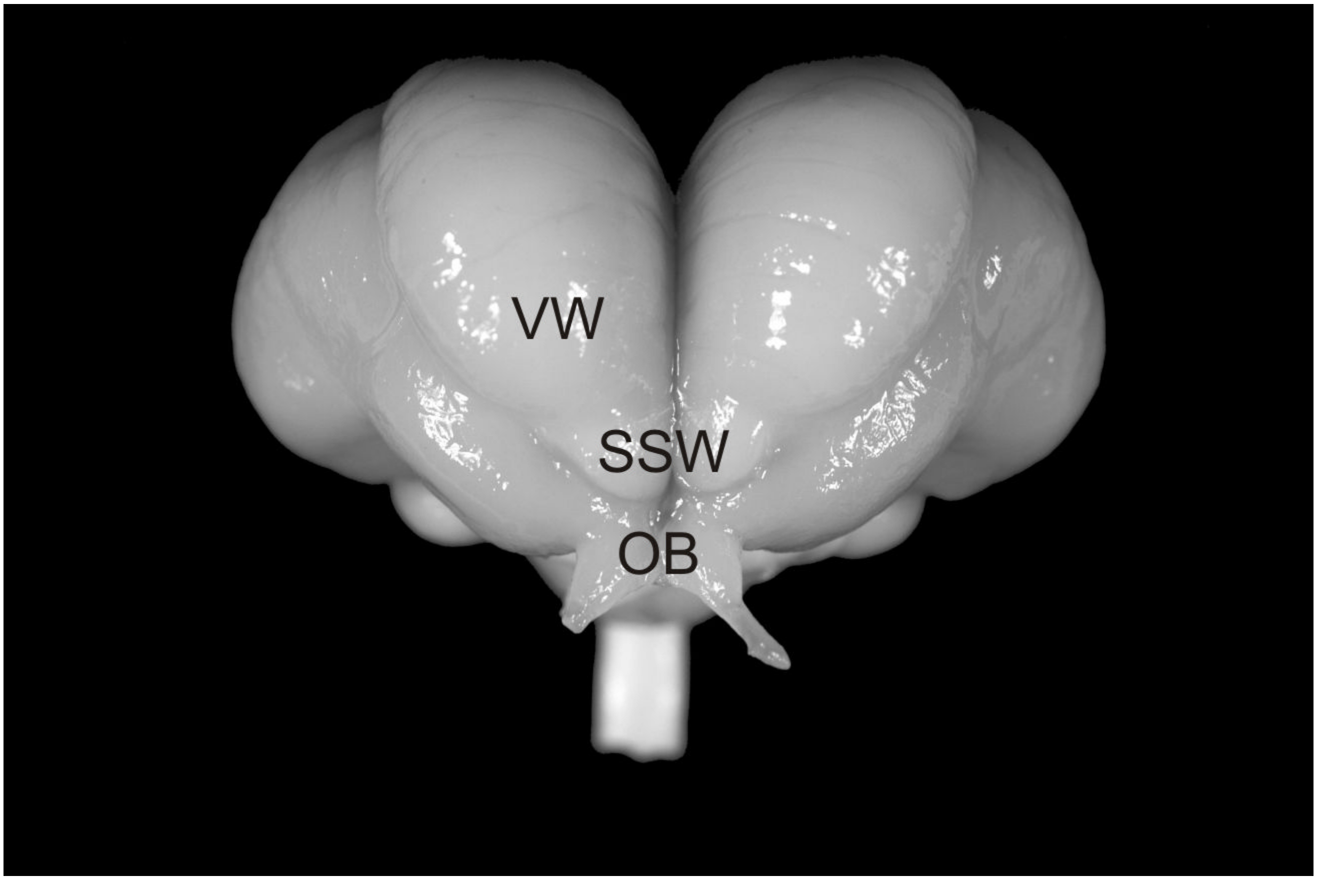

FIGURE 1.
Photograph of the brain of a barn owl viewed from in front. VW: Visual Wulst; SSW; somatosensory Wulst (claw area); OB: olfactory bulb.

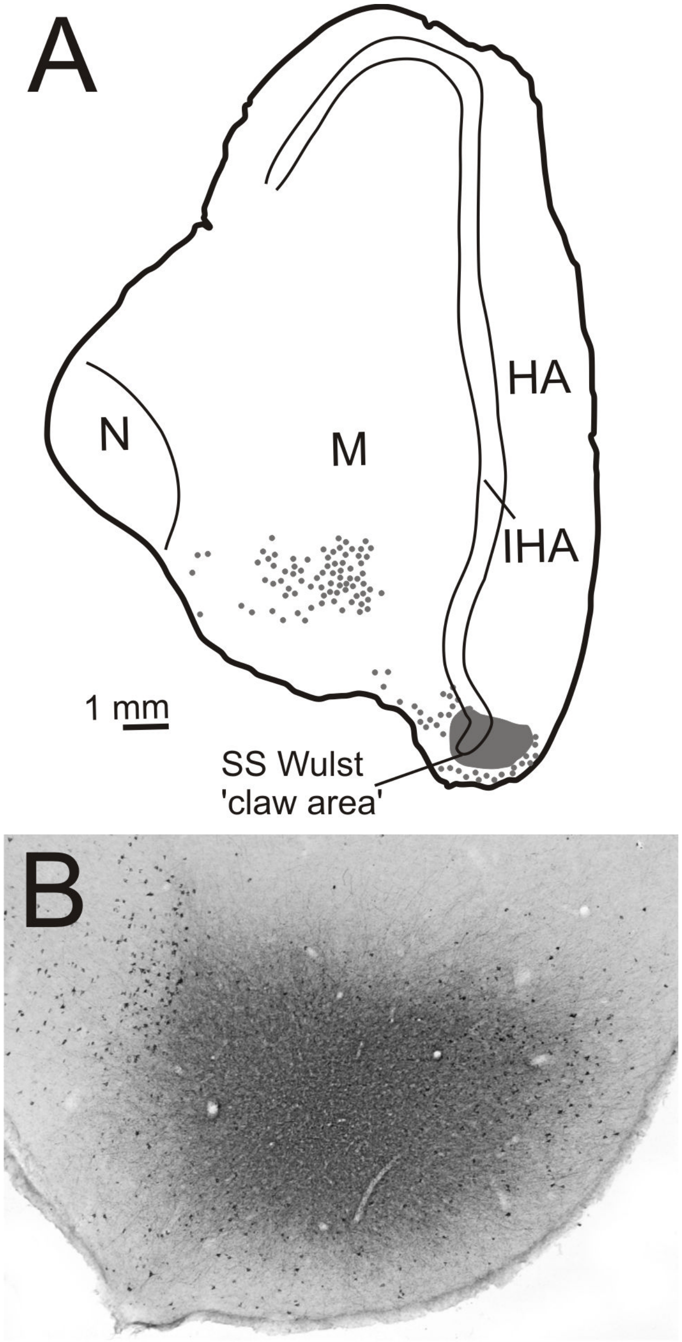

FIGURE 2.

A: Camera lucida drawing of a Nissl counterstained left hemisection through the rostral pole of the telencephalon, including the protuberance of the rostral Wulst, indicating the location of a CTB injection (solid grey) actually centered on - as defined by the track made by the injection pipette - the thalamorecipient layer IHA of the ‘claw area’, and retrogradely labeled cell bodies (dots) both close by and in the mesopallium (M). B: Photomicrograph of the CTB injection depicted in A.

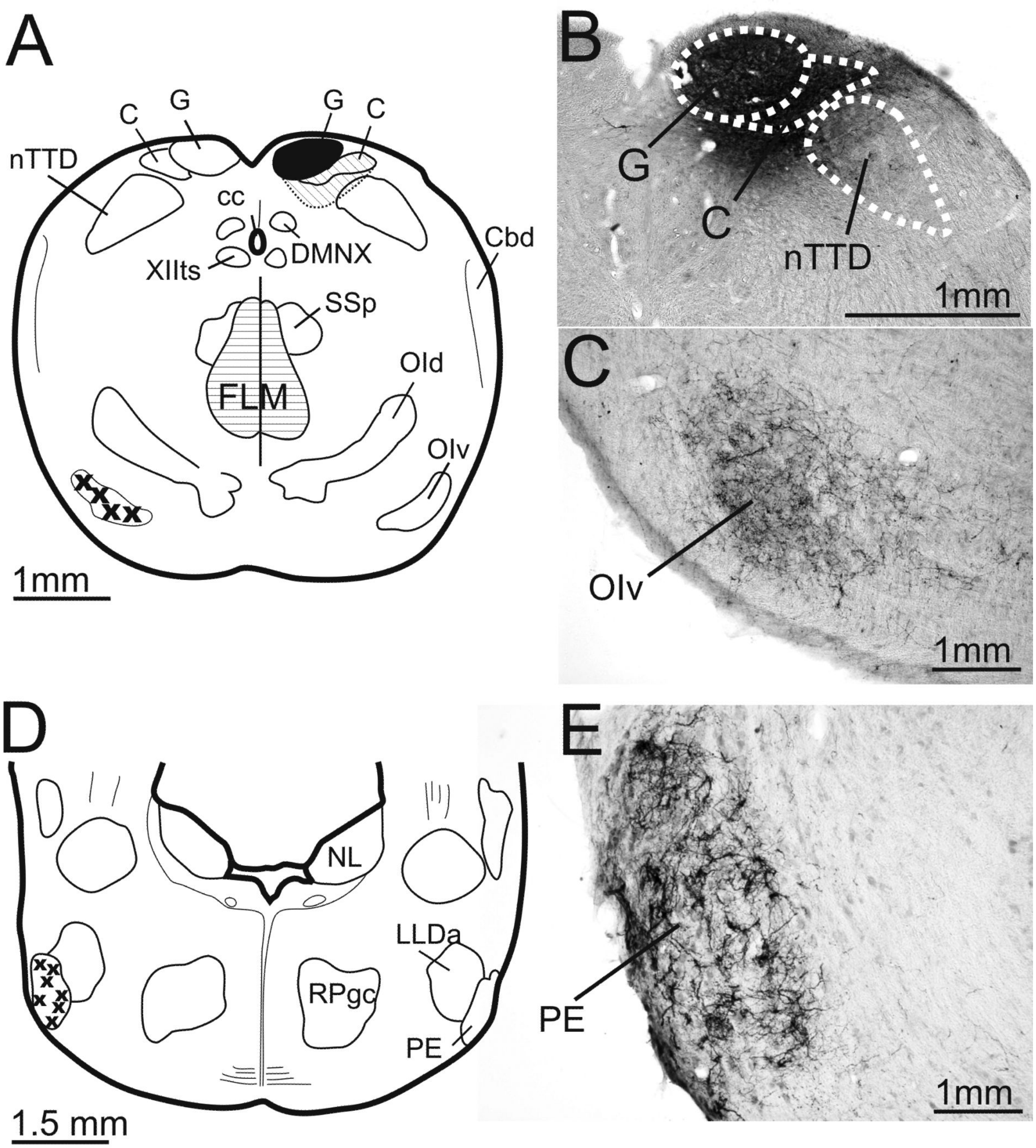

FIGURE 3.

Projections resulting from an injection of BDA in the DCN. Crosses in the schematics indicate the location of terminal fields. A: Camera lucida drawing of a Nissl counterstained, caudal medullary section through the injection site, a photomicrograph of part of which is shown in B. C: Terminal field in the contralateral ventral lamella of the inferior olive (OIv). D: Camera lucida drawing of a Nissl counterstained section through the pons depicting a terminal field in PE, shown in E.

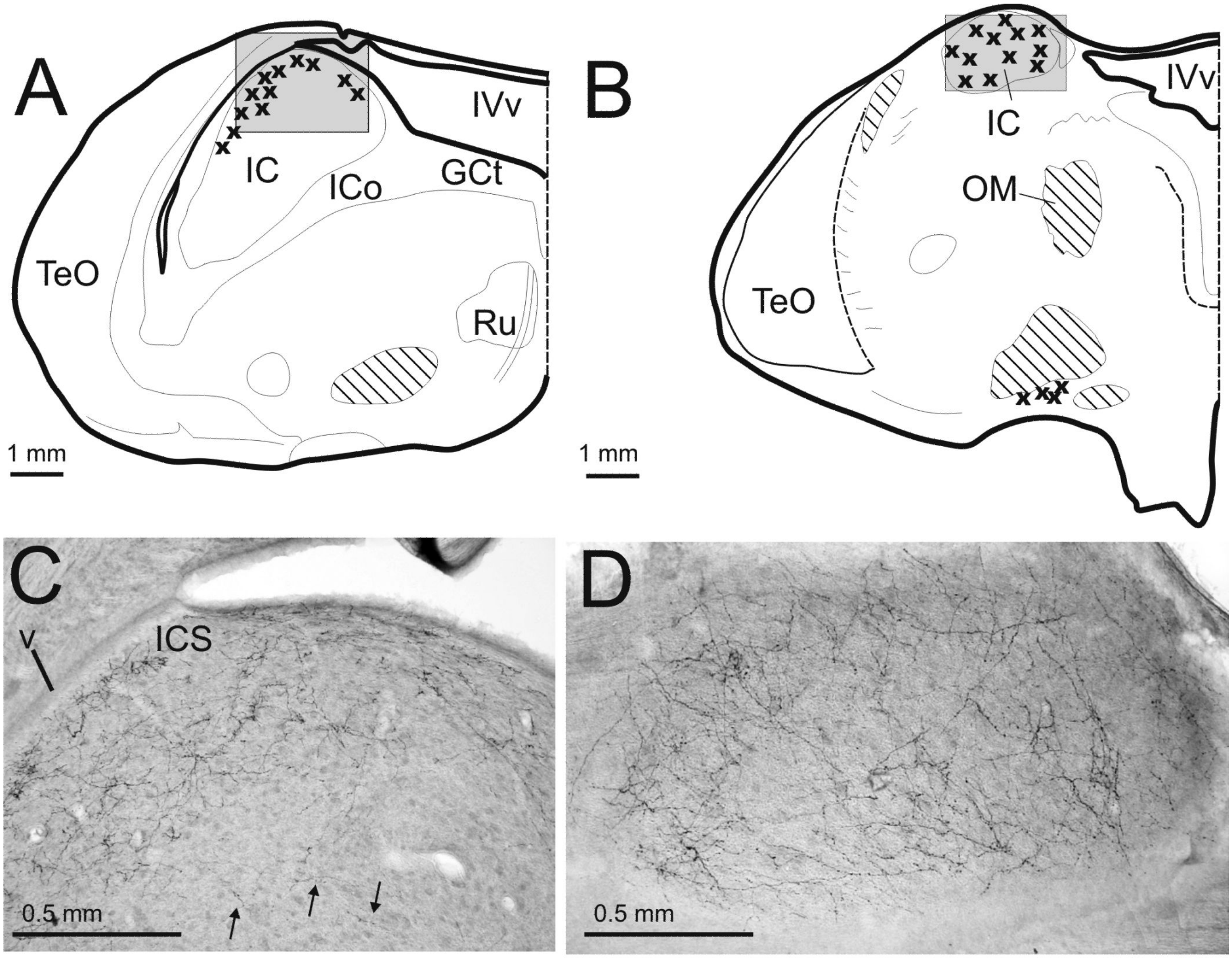

FIGURE 4.

Projections resulting from an injection of BDA in the DCN - continued. Crosses in the schematics indicate the location of terminal fields. A and B: Camera lucida drawings of Nissl counterstained left hemisections through the midbrain showing the location of terminal fields in the dorsal part (A) and rostral pole (B) of the inferior colliculus (IC; see text). A small terminal field is also present in the ventral midbrain in B. The fields in the grayed boxes are depicted photomicrographically in C and D. Arrows in C point to labeled fibers and terminations in the center of the IC. Major fiber tracts (e.g., OM) are depicted by oblique line shading.

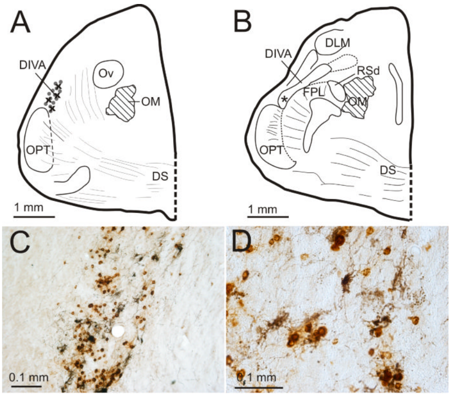

FIGURE 5.

Projections resulting from an injection of BDA in the DCN - continued - and retrogradely labeled cell bodies resulting from an injection of CTB into the rostral Wulst. A: Camera lucida drawing of a Nissl counterstained left hemisection through the thalamus showing the location of the terminal field (crosses) and retrogradely labeled cell bodies (filled circles) in the caudal part of DIVA. B: A similar depiction through a more rostral level of DIVA, the region of overlap of terminal field and labeled cell bodies being indicated by an asterisk. C and D: Photomicrographs of the overlap of fibers and terminations (black) and labeled cell bodies (brown) in DIVA; C is a relatively low power photo of the overlap region depicted in A, and D a relatively high power photo of the overlap region depicted by the in B.

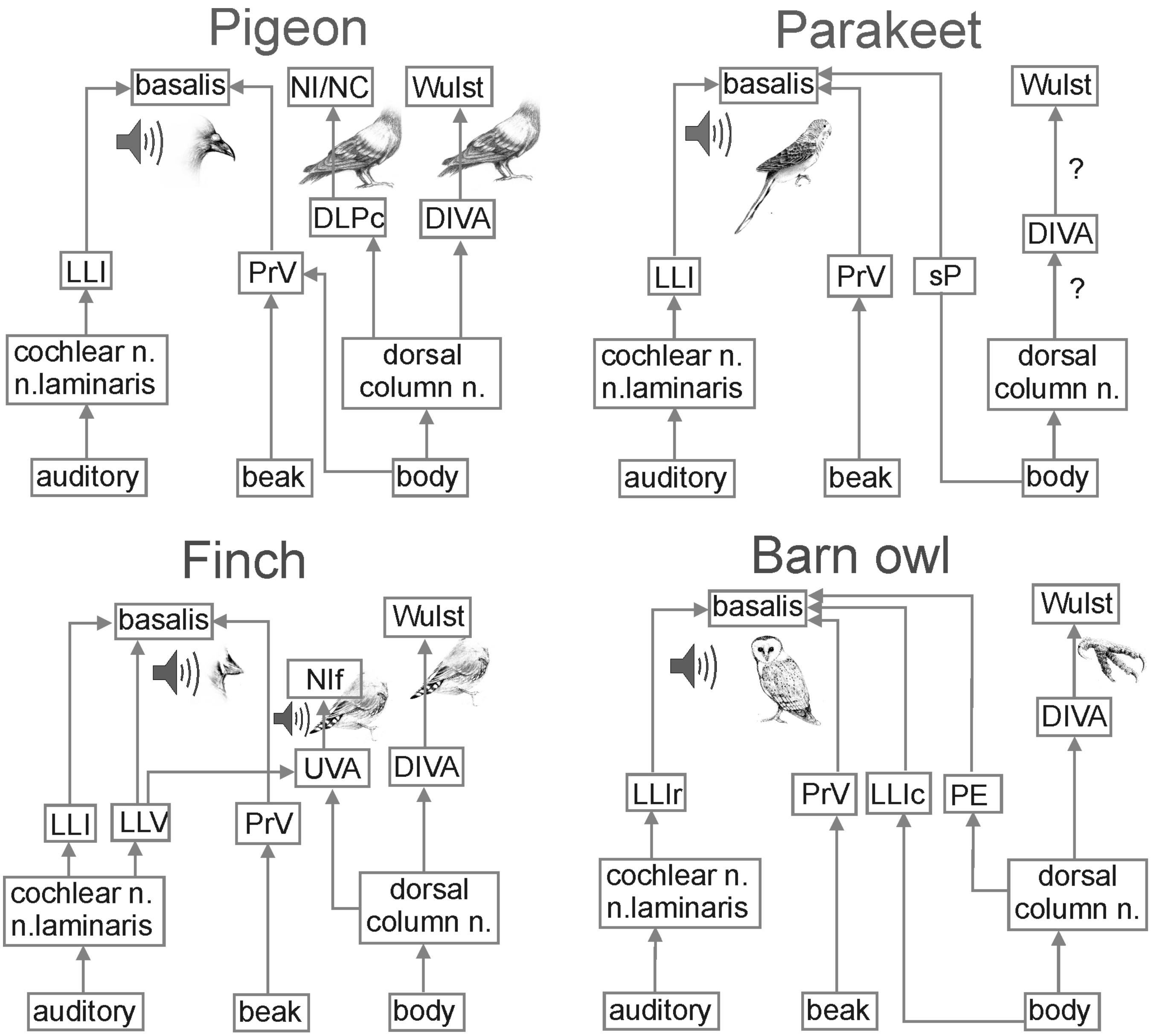

FIGURE 6.

Comparative schematic of ascending somatosensory and auditory projections to the telencephalon via thalamic and non-thalamic pathways in different avian groups. The data on which these projections are based are all derived from papers cited in the references. Note the ‘beakless’ representation of the body in the rostral Wulst of pigeons and finches and the complete body+beak+auditory representation in Bas of parakeets and barn owls (auditory representations are symbolized by loud speakers).