

birds (Fig. 7). Little information is available about motor control pathways of vocalization production in crocodylians.

(1) From cochlear nuclei to midbrain auditory nuclei

There are striking parallels between the ascending auditory pathways in the crocodylian and avian brain (Fig. 7). As in birds, Leake (1974) showed in spectacled caiman that the auditory nerve (VIIIth cranial nerve) conveys auditory information from the basilar papilla to the brainstem and projects topographically to two cochlear nuclei located in a rostro-caudal column in the dorsal hindbrain: the nucleus magnocellularis (NM) and the nucleus angularis (NA) (reviewed for birds in Burger *et al.*, 2005; Kubke & Carr, 2005). In crocodylians, the auditory nerve also has been reported to project to the nucleus laminaris (Soares, Simon & Carr, 1999). The functional organization of cochlear nuclei in the spectacled caiman is extremely similar to that of birds (Konishi, 1970; Manley, 1970), particularly in the organization of tonotopic maps. Crocodylian NA neurons of increasing frequency characteristics are distributed along three topographical axes (lateral to medial, rostral to caudal, and ventral to dorsal). The organization of the crocodylian NM is less clear than that of the NA (Manley, 1970). Both these features are found in birds, where the tonotopic organization of the NA (with a distinct vertical gradient) is clearer than that of the NM (see Konishi, 1970, for details). The lateral to medial frequency tonotopy in the NA is reversed in crocodylians relative to birds (Manley, 1970). In both crocodylians and birds, the tonotopic organization in the cochlear nuclei reflects the frequency representation and the sensitivity present in the basilar papilla. This similar arrangement suggests that the crocodylian cochlea performs frequency analysis in a way similar to birds.

In birds, the NM and NA nuclei initiate two parallel ascending pathways, with the NM computing temporal aspects (Monsivais, Yang & Rubel, 2000; Parks & Rubel, 1975) and the NA processing multiple features of the signal (Hotta, 1971; Köppl & Carr, 2003; Sullivan & Konishi, 1984). Similar information on how signals are processed is not available for crocodylians and it is thus not known if a similar functional distinction between the NM and the NA exists.

As in birds, the crocodylian brainstem auditory system includes two additional nuclei, the nucleus laminaris (NL) and the superior olivary nucleus (SON) (see Carr & Code, 2000, for a review). In both birds and crocodiles, the NL receives inputs from the NM and (at least in birds) is involved in processing interaural time differences (Carr & Konishi, 1990; Parks & Rubel, 1975; Soares *et al.*, 1999; Young & Rubel, 1983). In birds, NM afferents to NL function as delay lines and NL neurons act as coincidence detectors to create a map of interaural time difference (Christensen-Dalsgaard, 2007; Grothe *et al.*, 2004; Klump, 2000). The precise organization of projections from NM to NL varies with species. In the chicken *Gallus domesticus*, these projections are asymmetric (only the projection to the contralateral NL takes the form of delay lines), whereas in

the barn owl, a species highly specialized for sound localization, NM projections are symmetric (with delay lines in both the ipsilateral and contralateral NL) (Grothe *et al.*, 2004). Moreover, NL neurons are arranged tonotopically (Rubel & Parks, 1975) and present cellular specializations that may be critical to the frequency dependence of sound-source localization (Kuba *et al.*, 2005). As crocodylians show a well-developed NL (Carr & Code, 2000), it is possible that this nucleus plays an important role in sound localization.

In birds, the NA and NL project bilaterally to the SON, an auditory nucleus in the ventrolateral medulla and pons, located below the nucleus laminaris (Carr & Code, 2000; Conley & Parks, 1986; Westerberg & Schwarz, 1995). In birds, the SON provides inhibitory inputs to both the NM and NL that may serve as a “gain control” mechanism to increase the acuity of temporal integration (see Burger *et al.*, 2005, for detailed discussion of the inhibitory functions of the SON). A similar cochlear efferent system was shown in spectacled caiman (Strutz, 1981). As in birds, cochlear efferents are found in separate dorsal and ventral cell groups. The anatomical distribution of avian cochlear efferent neurons appears to have many features in common with crocodylians. Besides these descending projections, the avian SON sends ascending projections to: (1) the central nucleus of the auditory midbrain which corresponds to the inferior colliculus (also called nucleus mesencephalicus lateralis pars dorsalis in birds and frequently named the torus semicircularis in reptiles) and (2) to the dorsal nucleus of the lateral lemniscus (Carr & Code, 2000; Conley & Parks, 1986; Westerberg & Schwarz, 1995). The ascending neural circuitry of the SON in crocodiles is less known. In crocodylians, the NA and NL project bilaterally to the torus semicircularis (Carr & Code, 2000; Ten Donkelaar, 1998). In birds, these same two nuclei also project to the auditory midbrain (Boord, 1968; Conley & Parks, 1986). These projections are segregated within the central nucleus, as are the projections from the lemniscal nuclei (Boord, 1968; Carr & Code, 2000). The cytology and connections of the midbrain and thalamic components of the auditory system of spectacled caiman have been described (Pritz, 1974*a,b*). As in birds, the torus is composed of two distinct regions: an external nucleus continuous with the deep layers of the optic tectum, and a central nucleus. Also as in birds, the characteristic frequencies vary with recording depth in the torus, with low frequencies (70 Hz) represented superficially and high frequencies (1850 Hz) represented more deeply (Manley, 1971). Thus, the frequency tonotopic organization is maintained in auditory nuclei from the level of the cochlear nuclei to the forebrain. The lemniscal nuclei occur in a column in the ventral hindbrain, rostral to the SON and ventral to the auditory midbrain. Three lemniscal nuclei are present in birds, dorsal (LLD) intermediate (LLI) and ventral (LLV) (Carr & Code, 2000). Only dorsal and ventral lemniscal nuclei have been described in lizards (Ten Donkelaar *et al.*, 1987). In birds, the NA projects bilaterally to these three lemniscal nuclei and the NL projects contralaterally to the LLV and LLD (Carr & Code, 2000; Conley & Parks, 1986; Takahashi *et al.*, 1987). Similar data are lacking for crocodylians.