

condition. Higgs *et al.* (2002) examined the impact on hearing of the air bubble trapped in the external ear when the animal submerges. They showed that it has no effect on auditory thresholds suggesting that sound waves reach the alligator inner ear by a different pathway underwater as opposed to on land. These authors suggested that bone conduction may be a logical alternative pathway since in humans, at least, the skull is better coupled to water than to air.

In birds, the peak energy of vocalizations usually corresponds to the maximum sensitivity of the audiogram (Dooling *et al.*, 2000). As underlined by Konishi (1970), birds show interspecific variation in characteristic frequencies which is correlated to their hearing abilities and their range of vocal frequencies. As a result of co-evolution between emission and reception processes, this match between communication signal properties and sensory abilities appears to be a general rule in the animal kingdom (although the precision of the match may not be absolute). The same relationship may be true for crocodilians, e.g. the peak frequency output of hatchling alligators' calls is around 900 Hz, corresponding well with the region of best auditory sensitivity of the adult (Higgs *et al.*, 2002). However, further studies are needed to investigate the relationships between sound production and hearing abilities in crocodilians. In particular, does the sensitivity range change with age, together with the spectral characteristics of vocalizations (Vergne *et al.*, 2007)?

Crocodilians are poikilotherms with a wide thermal activity range (Diefenback, 1975; Garrick & Garrick, 1978). Their optimal temperature is around 29–35°C (Diefenback, 1975; Pinheiro *et al.*, 2001). Although most crocodilians inhabit tropical and sub-tropical regions where annual temperature varies little, several species have larger latitudinal ranges and may be exposed to temperature variations. For instance, in the northern extremes of its range, the American alligator may be exposed to temperatures below 0°C and its tolerance to temperature variations has been experimentally verified (Colbert, Cowles & Bogert, 1946). Even for tropical species, diurnal variation and weather conditions can lead to significant modifications in ambient temperature. The effects of temperature on crocodilian hearing process is thus of interest.

The effects of temperature on the responses of primary auditory fibres were investigated in young adult spectacled caimans by Smolders & Klinke (1984). They maintained the body temperature at a standard cloacal temperature of 27°C while the head temperature was changed from 10 to 35°C. The mean spontaneous firing rate of auditory fibres increased nearly linearly with temperature as did the characteristic frequency. Below 11°C, neural firing ceased (measured using a thermocouple inserted between the auditory nerve and the bony capsule of the inner ear). A temperature increase from 20 to 30°C was associated with a 10 dB threshold decrease and consequently an increase in auditory sensitivity. It is likely that these temperature-linked modifications in auditory perception would impair acoustic communication due to poor matching between auditory abilities and acoustic characteristics of emitted signals.

Indeed, Garrick & Garrick (1978) showed that the spectral composition of spectacled caiman calls was independent of temperature, unlike the situation in some amphibians where temperature-related audiograms are accompanied by appropriate changes in the call spectro-temporal composition (Hubl & Schneider, 1979). As it is likely to interfere with the perception of vocalizations, it is important to consider how much variation of body temperature occurs under natural circumstances. Crocodilians are able to thermoregulate using both behavioural (sun exposure, bathing) and physiological mechanisms (Colbert *et al.*, 1946; Diefenback, 1975; Smith, 1979). While smaller individuals will be more sensitive to temperature changes (Colbert *et al.*, 1946), large individuals are capable of producing sufficient metabolic heat to maintain preferred temperature range (Diefenback, 1975; Smith, 1979). However, there may be situations in which the body temperature fluctuates and may impair the optimal reception of acoustic signals. It would be interesting to investigate the influence of temperature in a species that has to cope with seasonal temperature fluctuations like the American alligator.

Conspecific interactions and predation require both detection and accurate acoustic localization of sound sources. In birds, several studies have documented the role of interaural intensity level and time differences in sound localization (Klump, 2000). Information on the capacity of crocodilians to localize a sound source is limited. Beach (1944) showed that American alligators are able to localize precisely the position of a sound source in air and water, but these initial observations have not been replicated and the physiological mechanisms underlying them remain unknown. Besides acoustics, it is possible that crocodiles in water can localize a sound source using dome pressure receptors located on their faces (Soares, 2002). We await scientific investigations documenting whether crocodilians can locate sound sources, and to decipher the underlying mechanisms.

IV. AUDITORY PROCESSING IN THE CENTRAL NERVOUS SYSTEM

The central nervous system of birds and crocodiles shares the same general (archosaurian) organization. The forebrain of birds and crocodiles is elaborated from a basic structure termed the dorsal ventricular ridge for which no comparable structure has been identified in mammals (Rogers, 1999). As in other vertebrates like mammals, the archosaurian forebrain is divided into three domains: pallium, striatum, and pallidum; the pallium being the site of complex cognitive capacities. A recent nomenclature of the avian brain emphasized that the pallium is the most developed area, being the interface between sensory inputs and motor outputs regulating behaviour (Jarvis *et al.*, 2005). Whereas there are extensive investigations of the structure and function of the avian brain, little is known about the functional organization of the crocodilian brain. Below we describe the ascending auditory pathways in crocodiles and