Chameleon Physiology

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3.1   NEUROPHYSIOLOGY

Sensory Physiology

The sensory system of chameleons is highly tuned toward visual stimuli. Not only do chameleons rely on visual signals in a social context, they are also visual predators (Gans, 1967). As such, a large body of literature has been devoted to the functioning and anatomy of the visual system. For example, it has been shown that chameleons have a negatively powered lens (Land, 1995; Ott and Schaeffel, 1995) and use accommodation cues to judge distance (Harkness, 1977), features convergent with the sandlance (Pettigrew et al., 1999). The auditory system has also been studied in some detail and shows lower hearing sensitivity as compared with that of other lizards (Wever, 1968, 1969a,b). Little is known about the physiology of the olfactory (smell), vomerolfactory, and gustatory (taste) systems in chameleons beyond anatomical descriptions (Schwenk, 1985; Halpern, 1992). In general, the reduced development of these systems is thought to be associated with reduced functionality, which is attributed to the highly visual nature of chameleons (Chapter 2).

Visual System

Chameleons rely heavily on the visual system for a wide variety of behaviors ranging from foraging and prey capture to social signaling and predator detection. Many of the unusual features of the eyes (e.g., their ability to move the eyes independently over 180 degrees horizontally and over 90 degrees vertically; Sándor et al., 2001), and of the visual system in general, have evolved in tight relationship with their unique ballistic tongues used during prey capture (Chapters 2, 4). Although initially it was believed that chameleons used

stereopsis (i.e., binocular vision) to judge distance (Duke-Elder, 1957), it was later demonstrated that prey distance is estimated using accommodation cues (i.e., changing of lens shape to maintain focus on an object as its distance varies; Ott and Schaeffel, 1995). Consequently, chameleons are capable of successfully capturing prey with one eye occluded (Kirmse et al., 1994). The accommodation range is large in chameleons, and the focusing precision is better than in other vertebrates (Ott and Schaeffel, 1995; Ott et al., 1998). Surprisingly, chameleons are similar to nonhuman primates in having a vestibuloocular reflex response that optimally stabilizes the entire retinal image (Haker et al., 2003). Although chameleons use independent eye movements to scan their environment directly preceding prey capture, chameleons use binocular fixation at the moment of prey capture (Flanders, 1985; Ott, 2001).

In addition to functional and physiological studies, a series of papers has investigated the neuroanatomy of the visual system in chameleons (Bennis et al., 2001, 2005). The neuronal organization of the visual system in chameleons suggests several features unique to chameleons. First, the ipsilateral retinofugal projection is absent; second, an additional hypothalamic visual center is present; and third, the nucleus opticus tegmenti is unusually large as compared with other lizards (Bennis et al., 1994; 1996). Studies on the optic nerve and retina show that chameleons have a complex retina that is in some ways similar to the mammalian one (El Hassni et al., 1997; Bennis et al., 2005). Moreover, the retina possesses four distinct types of single cones (Bowmaker et al., 2005), rendering the visual system of chameleons sensitive to visible light and the near ultraviolet with a cutoff at about 350 nm (Hunt et al., 2001; Bowmaker et al., 2005). This suggests that signaling in the ultraviolet range may make up an important component of the behavioral repertoire in chameleons (Stuart-Fox and Moussalli, 2008; Chapter 6).

Auditory System

Several studies have been devoted to the auditory system of chameleons (Wever, 1968, 1969a,b). Chameleons are unusual in having no external ear opening and no visible tympanic membrane. Moreover, the round window of the cochlea is lacking (Wever, 1968). Consequently, chameleons have a relatively poor auditory sensitivity as compared with other lizards (Wever, 1968, 1969a). Interestingly, different auditory sensitivities were recorded for species of the genus *Chamaeleo* versus the genus *Trioceros,* with *T. hoehnelii* and *T. jacksonii* having poorer auditory performance than all species of *Chamaeleo* (Wever, 1968, 1969a). Moreover, severing of the columella decreased hearing performance in species of the genus *Chamaeleo* but not *Trioceros.* This was explained by a difference in the sound-reception mechanisms in the two genera. Whereas aerial sounds are received by the pterygoid plate embedded in the tissues at the side of the head in species of *Chamaeleo* (Wever, 1968, 1969b), this system is dysfunctional in *Trioceros* because of the lack of the anterior process of the extracolumella (Wever, 1969a). Although at the time it was unknown that these species with different morphologies belonged to different genera (Townsend and Larson, 2002; Chapter 7), this observation suggests a strong phylogenetic effect. Unfortunately,

given the lack of data for other genera, the basal condition of the group cannot be deter-mined. Moreover, whether the difference in anatomy and hearing sensitivity is related to differences in habitat use (with *Trioceros* typically being forest dwellers) remains unknown.

Sleep

Although in general, relatively little is known about sleep in reptiles, one study has inves-tigated sleep in chameleons (Tauber et al., 1966). One of the big debates in the literature is whether rapid eye movement (REM) sleep is present in reptiles other than birds (Tauber et al., 1968; Siegel, 2008). Although the evidence is equivocal, most studies tend to suggest that, although reptiles do sleep, no true REM sleep can be demonstrated based on recordings of brain activity (Ayala-Guerrero and Mexicano, 2008; Siegel, 2008). Yet, Tauber and colleagues (1966) demonstrated an intriguing pattern of eye movements in cha-meleons during physiological sleep states. Specifically, they demonstrated that typically brief periods of REM are present while sleeping. Unilateral eye movements with the eyelid opened are also observed without any changes in sleep posture. However, their electroen-cephalographic recordings from the telencephalon suggested no true REM sleep is present. Given the radically different anatomy of the lizard brain, recordings from the brain stem (where the structures homologous to those recorded in mammals and birds reside) would be needed to confirm this. In conclusion, neurophysiological studies in reptiles are woefully lacking behind those of other vertebrates and much remains to be investigated.

3.2   MUSCLE PHYSIOLOGY

Studies on chameleon muscle physiology are rather scarce and can be subdivided into two groups: those that investigate the physiological basis of the slow locomotion in chameleons, and those interested in the structure and physiology of the tongue muscles. Chameleons are well known for being slow, with sprint speeds being about 10 times slower than those of closely related agamid lizards of similar size (Abu-Ghalyun et al., 1988; Losos et al., 1993; Herrel et al., 2011; see also, Chapter 4). To better understand the physiological basis of this slow locomotor behavior, several studies have examined the histochemical, ultrastructural, and metabolic profiles of chameleon muscle (Guppy and Davison, 1982; Abu-Ghalyun, 1990; Mutungi, 1992). These studies show that chameleons possess, on average, more slow fibers in the arm and leg muscles as compared with other lizards (Abu-Ghalyun, 1990; Mutungi, 1992). Moreover, fast lizards such as skinks have higher metabolic potential in skeletal and cardiac muscle than chameleons, yet both skinks and chameleons have mammalian-level metabolic capacities, as indicated by levels of citrate synthase and β-hydroxybutaryl-coenzyme A dehydrogenase in the heart (Guppy and Davison, 1982). The slow locomotion of chameleons thus likely resides in the contractile capacities of its locomotor muscles (Abu-Ghalyun et al., 1988) coupled with the changes in limb posture (Chapter 4), and lower overall muscle mass as compared with that of other lizards of similar size (A. Herrel, personal observation). The contractile properties of the iliofibularis muscle

show generally slower (up to four times slower) contraction velocities as compared with similarly sized agamids (Abu-Ghalyun et al., 1988).

In contrast to the limb muscles, the tongue muscles of chameleons are anything but slow. Indeed, histochemical profiling revealed only fast glycolytic and fast oxidative glycolytic fibers in the tongue muscles (Herrel et al., 2001b). Consistent with this observation, muscle innervations were always of the "en plaque" type (Herrel et al., 2001b). Muscle-physiology experiments showed that the tongue retractors in chameleons are somewhat slower than those in closely related agamid lizards (time to peak tension, 42 vs. 23 ms; time to half relaxation, 35 vs. 23 ms), yet they produce high forces for their cross-sectional area (Herrel et al., 2001a, 2002; Anderson and Deban, 2013). Chameleons have unusual tongue-retractor muscles that are of the supercontractile type (Rice, 1973; Herrel et al., 2001a , 2002, 2009). These muscles are characterized by perforated Z discs and high, nearly invariant force-generation capacity over a wide range of muscle lengths (Herrel et al., 2001a, 2002). Despite the thermal independence of overall tongue projection (Anderson and Deban, 2010), the physiology of the accelerator muscle responsible for tongue projection is highly temperature-dependent (Anderson and Deban, 2013). Thus, the reduced thermal sensitivity of tongue-projection performance appears to be the result of the morphologic arrangement and the incorporation of elastic elements into the projection mechanism rather than physiological specialization of the associated muscles (Anderson and Deban, 2013).

3.3   METABOLISM, SALT, AND WATER BALANCE

Surprisingly few studies have investigated the metabolism of chameleons (Burrage, 1973; Wheeler, 1984; Zari, 1993). Given their slow sit-and-wait or cruise foraging behavior and generally cryptic lifestyle (Butler, 2005; Chapter 5), chameleons could be expected to have low standard metabolic rates. Yet, metabolic rates of chameleons are similar to those measured for other lizards and are highly dependent on body mass (Burrage, 1973; Bennett and Dawson, 1976; Andrews and Pough, 1985; Zari, 1993). Moreover, standard metabolic rate is highly temperature-dependent, with Q_{10} values of 3.38 to 3.81 in the range from 20 to 30°C for *C. calyptratus* (Zari, 1993) but with lower Q_{10} values for *C. namaquensis* and *B. pumilum* (1.26 to 2.91) (Burrage, 1973). Interestingly, for the desert-dwelling species (*C. calyptratus* and *C. namaquensis*) Q_{10} values decrease above 30 to 35°C, suggesting an adaptation to their hot desert environment (Burrage, 1973; Zari, 1993). One study investigated the water relationships and dehydration rates of chameleons (Burrage, 1973). Differences between species were observed in dehydration rates with the desert-dwelling *C. namaquensis* dehydrating much more slowly than *B. pumilum* (note that the *B. pumilum* included in the study by Burrage, 1973, are likely individuals belonging to both *B. pumilum* and *B. occidentale*). Furthermore, the *C. namaquensis* excreted salt around the nares suggesting the presence of salt glands (Burrage, 1973). This has been suggested to be an adaptation of desert-dwelling lizards that feed on halophytic plants (Norris and Dawson, 1964) and/or the presence of cloacal water reabsorption (Schmidt-Nielsen, 1963).

3.4   TEMPERATURE

Chameleons are found among widely varying thermal regimes and climatic conditions ranging from hot and dry desert habitats, through tropical rainforests and Mediterranean climates, to high-altitude environments (Burrage, 1973; Hebrard et al., 1982; Reilly, 1982; Bennett, 2004; Chapter 5). Although chameleons are often described as being thermoconformers (e.g., Dimaki et al., 2000), more recent studies show that chameleons carefully regulate body temperatures using behavioral thermoregulation and color change to maintain temperatures of around 30 to 32°C (Bennett, 2004; Andrews, 2008). The preferred temperatures of chameleons are low compared to those of most other diurnal lizards, including closely related agamid lizards (Burrage, 1973; Andrews, 2008a,b) suggesting an adaptation to lower temperatures. This, in combination with the temperature-invariant function of the ballistic tongue protraction (Anderson and Deban, 2010) may have allowed chameleons to invade high-mountain habitats rarely accessible to other lizards. Moreover, chameleons in cold environments will change skin reflectance at low temperature, allowing them to heat up more rapidly and thus reduce time spent basking (Burrage, 1973; Walton and Bennett, 1993).

3.5   SKIN PIGMENTATION, COLOR CHANGE, AND THE ROLE OF ULTRAVIOLET LIGHT

Despite the long-standing interest in color change in chameleons dating back to Aristotle (350 BC), surprisingly few studies have investigated the mechanism of color change in chameleons (Brücke, 1852b; Hogben and Mirvish, 1928; Zoond and Eyre, 1934; Canella, 1963). The current consensus is that melanophores and other chromatophores in the skin (e.g., xanthophores, erythrophores and iridiophores; see Cooper and Greenberg, 1992) are under the control of the autonomic nervous system (Berger and Burnstock, 1979; but see Canella, 1963, for a possible example of hormonal color change in *T. jacksonii*) unlike those in, for example, amphibians, which are typically under hormonal control (Hogben and Slome, 1931; Camargo et al., 1999). It is thought that the melanophores are maintained in a state of tonic contraction that is inhibited by light (Zoond and Eyre, 1934). In addition, visual stimuli may suppress the tonic contraction of the melanophores, resulting in color change and background matching (Zoond and Eyre, 1934). The light-dependent color change allows chameleons to optimize heating rates and minimize basking time (Walton and Bennett, 1993). However, basking may play a role not only in thermoregulation, but it has also been suggested to play a role in the regulation of the vital hormone vitamin D_3 in chameleons and other lizards (Ferguson et al., 2003, 2005; Karsten et al., 2009a). Vitamin D_3 has an important function in the calcium–phosphorous hormonal regulation system enhancing calcium uptake through the gut when calcium levels are low (Ferguson et al., 2003, 2005). Finally, the nervous control of the chromatophores allows rapid color change. Consequently, color change is important in social-signaling contexts and is thus likely under strong sexual selection (Berger and Burnstock, 1979; Stuart-Fox and Moussalli, 2008; Chapter 6).

3.6 DEVELOPMENTAL PHYSIOLOGY

A considerable body of work has been devoted to the effects of temperature on egg development and growth in chameleons. Chameleons are unusual because in some species embryos are in the gastrula stage at the time of oviposition and may remain at this stage for several months (Bons and Bons, 1960; Chapter 5). The duration, and end, of this so-called embryonic diapause is dependent on temperature but not on moisture (Andrews and Donoghue, 2004; Andrews et al., 2008; Adams et al., 2010). Temperature also affects speed of development, growth of the yolk sac, as well as the final hatching phenotype (Diaz-Paniagua and Cuadrado 2003; Andrews, 2007, 2008; Diaz-Paniagua, 2007). Lower temperatures result in longer developmental times and larger hatchlings (Diaz-Paniagua and Cuadrado, 2003; Diaz-Paniagua, 2007). Temperature also affects the physiology and anatomy of the amnion and the rhythmic contractions thereof during development (Nechaeva et al., 2005). Although the function of these contractions is poorly understood, it is thought that they help mix the amniotic fluid, thus preventing adhesion between the embryo and the amnion (Romanoff, 1960). Hatching success is also dependent on temperature, being higher at low temperatures (Diaz-Paniagua and Cuadrado, 2003). Interestingly, the duration of the cold period is determinant. Periods of colder temperature of intermediate lengths produced the largest offspring (Diaz-Paniagua, 2007). Moderate temperatures also provide optimal embryonic and posthatching development in desert species such as *C. calyptratus* (Andrews, 2008). The temperature to which eggs are exposed during development does not, however, affect subsequent sprint performance or selected body temperatures (Andrews, 2008). The access of females to ultraviolet light has been shown to be important and to affect the development and hatching success of the eggs (Ferguson et al., 2002). Moreover, essentials vitamins such as vitamins A and E have been detected in eggs of chameleons (Dierenfeld et al., 2002), suggesting an important contribution of maternal effects to hatchling development, growth, and survival. Finally, developmental temperature in chameleons does not affect hatchling sex ratio in *C. calyptratus* and *F. pardalis,* indicating that chameleons most likely all have genetic sex determination despite scattered reports to the contrary (Andrews, 2005).