Cover illustration: A roving eye . . .

The Parson's chameleon (*Calumma parsonii*) is one of the largest and most robust chameleons, the males growing to a maximum of 65 cm in length. Madagascar is home to the Parson's chameleon, as well as over two thirds of the world's chameleon species. These peaceful, lethargic reptiles are stealth predators that can remain motionless for hours awaiting their prey. Their adaptations for predation are most startling.

The name "chameleon" betokens a veil of secrecy and mystery. Recent research on these interesting creatures, though, begins to draw this veil aside to reveal extraordinary physiological gifts.

The common currency of reptile folklore would have us believe that chameleons change colour in response to their background, but this is not true. Although the animal relies upon its camouflage to escape detection in some situations, it changes colour in response to mood, temperature, and light intensity but not according to its background. Aggressive territorial colour displays are common among males but other social displays, including courtship and species recognition, also rely heavily upon colour change. To accomplish these remarkable changes, chameleons have a complex skin structure. True chameleons have three types of chromatophores in their skin including xanthophores containing yellow or red pigmentation, melanophores containing melanin, and guanophores that reflect blue light but do not contain true pigment. The xanthophores are found in the superficial dermis and the melanophores are in the deeper dermis, with the guanophores beneath the melanophores. The melanophores project dendritic processes through the dermis upward towards the epidermis which is transparent or translucent. The skin colour is controlled neurologically and hormonally by the expansion or shrinkage of the xanthophores in combination with the movement of melanin vertically through the dermis. With the combination of blue from the reflecting substrate, dark brown or black from the melanin, and red or yellow from the xanthophores, almost any colour can be duplicated by the contraction or expansion of cells combined with the movement of melanin. The range and speed of colour change is unrivalled in the vertebrate world.

Using its prehensile tail, slender body, and its zygodactyle feet (grasping feet that look like two-finger mittens but really are bunched toes, with two toes in one bundle and three toes in the other), a chameleon will remain motionless and unnoticed on a branch indefinitely, moving only its turret-like eyes, eyes which have special qualities.

The chameleon has an ocular device unique in the animal kingdom. The crystalline lens of the chameleon is a minus lens! There is an evolutionary trend towards increased corneal power and decreased crystalline lens power as animals evolve towards better visual acuity. The chameleon has taken this to an evolutionary extreme, leading to a myopic lens. This optical configuration provides for a larger retinal image size on a comparative basis (Ott M *et al Nature* 1995;373:692-4). In effect, chameleons have produced a mini telephoto lens system.

These eyes appear bizarre because the eyelids are fused open as well as fused to the eye itself, allowing for a comparatively small opening and the external visualisation of only the pupil of each eye. Chameleons perform independent, unocular scanning saccadic and pursuit eye movements with each eye. One eye may remain still and unmoving while the other eye will scan the environment with a disjunctive ocular movement until a potential prey is located. Prey is generally insects but large chameleons can take small birds or mammals. Unocular accommodation with the roving eye is performed to assess distance during the scanning process, especially when prey is located. These large and independent saccades are a product of the same set of extraocular

muscles in other tetrapods and are very similar to our own, which means that Hering's law of equal innervation cannot be valid for this animal. Once potential prey is located within the known capture distance, simultaneous binocular activity begins until both eyes are yoked neurologically, but stereopsis does not occur, at least as we understand it. Coupled and identical accommodation occurs only shortly before the strike to confirm the correct distance from the tip of the mandible. Accommodation ranges are large—up to 45 dioptres—and very rapid—up to 60 dioptres per second—resembling the speed and amplitude of accommodation in birds. This is accomplished by the use of striated muscle rather than smooth muscle for accommodation. The retinal image plane is the most important cue used to measure distance to prey, and this projection onto the retina is achieved through precise accommodation. The large and very rapid range of accommodation allows for focus on near objects with great precision, coinciding with the projection length of the tongue. The chameleon is a visual predator with a well developed convexiculate fovea to mediate increased visual acuity,

but may not use the primary fovea for target fixation. Binocular, but not foveal, fixation of the prey is achieved with target projection onto the retina temporal to the fovea with a slightly divergent gaze position. Chameleon retinal ganglion cell maps reveal a horizontal visual streak and a second visual area temporal to the macula where the image is probably located

during this phase of prey capture. Chameleons use the cues from independent binocular accommodation rather than stereopsis to determine and confirm distance (Ott M *et al J Comp Physiol A* 1998;182:319-30). At that instant, the chameleon prepares for the strike, and it strikes with a most spectacular tongue.

The chameleon's tongue represents a physiological masterpiece. Tongue protraction for prey capture is often longer than the body length of the chameleon and is accomplished by a most unusual muscular system. Once prey distance is confirmed, "stalking" begins with the initial protrusion phase of the tongue. The tongue, or hyobranchial apparatus, includes several muscles and a cartilaginous entoglossal process surrounded by an accelerator muscle. After the prey is visually located and confirmed, the tongue is brought forward in the mouth and steadied. The large club-like tip of the tongue is projected just beyond the mandible. Immediately before projection the posterior portion of the accelerator muscle contracts against the entoglossal process with a biphasic activity pattern. This radial accelerator muscle has spiral fibres that achieve hypercontraction, rapidly flattening against the entoglossal process and pushing the tongue forward with the help of lubrication surrounding the tip of the entoglossal process. Remember, muscle volume remains constant so that when the muscle contracts the volume must be transferred. The force builds for approximately a tenth of a second before creating a spring-like effect, projecting the tongue in ballistic fashion (Wainwright PC, *J Exp Bio* 1992;168:1-21.) Although the mechanism of projection is not completely understood, the biphasic activity probably adds to the spring-like nature of the muscular force. The act is akin to squeezing a watermelon seed between your fingertips to "fire" it, but in this case, the seed remains motionless and the muscles are fired. The tip of the tongue is sticky, capable of suction, and is even capable of grasping the prey at its tip, by rapid invagination. The speed of the tongue projection is remarkable, with full extension of up to 14 cm in one sixteenth of a second. The photograph on the right hand side of the cover reveals the moment of capture for one hungry chameleon.

All this begins with a roving eye, looking for dinner.—Ivan R Schwab, MD, UC Davis Department of Ophthalmology, 4860 Y Street, Ste 2400, Sacramento, CA 95817, USA (Irschwab@ucdavis.edu).