Cover illustration

Look before you leap

There is something bucolic about frogs. Our almost universal fascination with them and their thoroughly endearing characteristics is probably responsible. Don't be fooled though by their beguiling nature, because frogs have valuable lessons to teach us about ocular evolution, visual processing, and binocularity.

Members of the class Amphibia, from the Greek meaning "double life," represent intermediate steps from an aquatic life to a terrestrial one that probably occurred during the late Devonian period, approximately 375 million years ago. Somewhere between *Ichthyostega*, a long extinct, tetrapod predator, and the coelacanth, a lobe finned fish, vertebrates first came ashore. These early amphibians breathed air, but were dependent for their reproduction upon water. All three extant orders of the class Amphibia—Anura (frogs), Urodela (salamanders), and Caecilia (a group of blind worm-like animals)—retain that echo of evolution, since all require water for their eggs and early developmental stages.

Both frogs and salamanders retain accommodative mechanisms resembling those of cartilaginous fishes, but many frog species seem to have lost the range of colour vision that salamanders still retain. Perhaps, for the frogs, it was the adaptation of a more nocturnal lifestyle and the "use it or lose it" evolutionary principle. Similarly, frogs probably lack the acuity of salamanders but have gained a more acute movement sense with concomitant nocturnality. Frogs have no fovea, and only a few species even have a concentrated area sophisticated enough to be considered an area centralis, an analogue of the macula. That said, though, there are other interesting adaptations to consider.

As frogs evolved, they developed a retractor globis muscle that retracts the eye into the orbit and since there is no bony structure between the eye and the oesophagus, this muscle is actually used to help swallow food. If you watch a frog swallow, you will note that, in many species, the eye "disappears" as the lids close over the eye, the animal using these muscles, and, in essence, the eyes, to swallow food. Despite the thin sclera, the eye literally pushes the food into the stomach.

Figure 1 *Osteocephalus taurinus* female near to tadpole in figure 2.

Figure 2 *Osteocephalus taurinus* tadpole with resorbing tail.

Pupillary differences evolved as well, but are not completely understood. All salamander pupils are round, but many frogs have unusual and peculiar shaped pupils. Little evidence exists as to purpose of the vertical, horizontal, or even heart-shaped pupils. Presumably these odd pupils relate to improved diurnal vision for a rod retina, or prey capture, but the answers to these questions are unknown.

Ocular optics evolved as well, as terrestrial life was embraced. The frog's corneas are steeper and smoother than those of fish, suggesting the early adaptation to terrestrial life. The amphibian predecessor that came ashore during the late Devonian brought with it many of the piscine visual adaptations and some of these may have presented problems for a newly terrestrial animal. For example, most fish have a completely crossed chiasm and yet higher terrestrial vertebrates, and especially predators, have a partially decussated chiasm with splitting of the fibres from each eye to each side of the brain. So, what happened, and how did this change occur?

In many ways, frogs represent a real and metaphorical bridge between aquatic and terrestrial, and certainly come from early tetrapod aquatic stock. The aquatic link is represented in the tadpole, as it is entirely aquatic, and has a completely crossed chiasm—just like fish. Presumably, when tadpoles develop they send the neuronal fibres from the eye to the contralateral optic tectum (the homologue to the mammalian superior colliculus) under the same or similar developmental stimulus as fish. The transition to frog, though, requires that the tadpole send new neuronal fibres from the retina towards the chiasm, where something most astonishing occurs. Genes at the chiasm, with the curious names of netrins, ephrins, semaphorins and slits, produce proteins that direct the migration, connectivity, and growth cessation of these new neurons (note, at this stage they are called neuronal growth cones) as they pass through the chiasm. The temporal fibres are directed to the ipsilateral brain and the nasal fibres to the contralateral side. These genes must turn their proteins on and off at the correct time to stimulate crossing or prevent recrossing and only in the appropriately selected fibres. Other related genes must tell the fibres to stop at their appropriate rendezvous, and at that point must also direct the correct topographical distribution within the tectum. Specifically, the ventral nasal fibres of, say, the left eye, must arborise with the next neuronal layer in the tectum precisely adjacent to the arborisation of its retinal neighbours necessary for the patterning of binocularity. Yet, this would be substantially different for the developing frog since the tadpole has a completely crossed chiasm and would have had very different signalling in its chiasmal and tectal development.

So, with amphibians, tetrapods "leapt" into a terrestrial and predatorial lifestyle and forever changed the visual system.

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Pictures by the author.