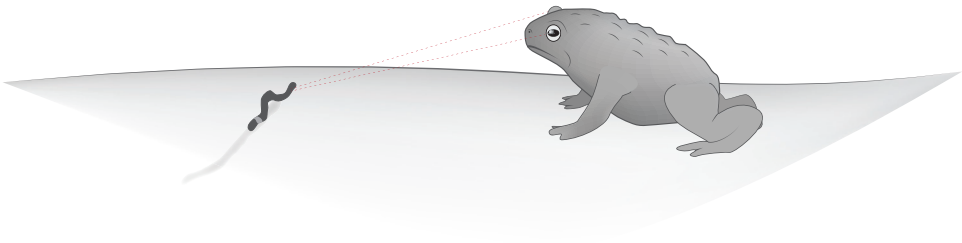


The Neuroethology of Predation and Escape

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CHAPTER 1

Vision



Very few species of animal are active only in complete darkness. At any moment in time, half of our planet is bathed in light radiating from the sun, while the other half remains partially lit by reflections from the moon, distant starlight, bioluminescence and human light pollution. It is thus unsurprising that many animals make use of some form of **vision** to provide information about the environment. Vision often provides the earliest cues for the detection of a predator or prey; it usually has a longer range than hearing, and is more precise and immediate than smell. Even when other sensory modalities do take the lead, vision is almost always additionally involved in the pursuit of prey, the guidance of a predatory strike or the coordination of an escape manoeuvre.

The information provided by vision depends on the complexity and sophistication of the eye, but even the simplest eyes are adept at detecting changes in light intensity, and these temporal cues are often important signals warning of the approach of danger. Many animals, particularly sessile forms such as barnacles, tubeworms or bivalve molluscs, display a **shadow withdrawal reflex** in response to a sudden dimming of the light. In these cases, the image detail is irrelevant, and it is the overall level of environmental illumination that matters. However, for many other animals, the image is crucial, because it enables the eye's owner to determine where the object of interest is located. Indeed, some authorities argue that it was the evolution of image-forming eyes, and a consequent step increase in the speed of the predator-prey arms race, that led to the massive proliferation in animal diversity about 540 million years ago, known as the **Cambrian Explosion** (Parker, 1998).

In this chapter, we will cover some of the key case studies in neuroethology that have informed our understanding of how animals use vision to detect, identify and respond to predators and prey. We first outline important principles of visual processing, including properties of light and the concepts of foveae, acuity and sensitivity. We then look at how meaningful features of an image are extracted as information passes through the visual pathway, in order to identify objects as predator or prey, using the toad as a model system. In the next part of the chapter, we outline the neurobiology of infrared vision in snakes. These ambush predators possess a highly specialised infrared visual system used to detect and target their warm-blooded prey. Finally, we will look at specialisations of the visual system in aerial predators that enable them to capture prey while simultaneously coordinating flight, using dragonfly vision as an exquisite example.

1.1 The electromagnetic spectrum

Light is a form of electromagnetic radiation (Figure 1.1) that consists of waves of energy that radiate through the air¹ at roughly 300 000 km/s. The intensity of light is determined by the amplitude of these waves, while what we perceive as colour is encoded in their wavelength.

For many animals, including humans, visible light spans a range of wavelengths between approximately 390 nm and 700 nm (the **visible spectrum**; Figure 1.1). We perceive these wavelengths as the colours of the rainbow, and we are able to do so because we

¹The speed of light varies slightly, depending on the refractive index of the medium through which it propagates. For instance, it is slower in water than air. The change in the speed of light can cause light rays to bend at the interface between different media – a process called refraction. This is an important aspect of the focusing mechanism in many eyes.

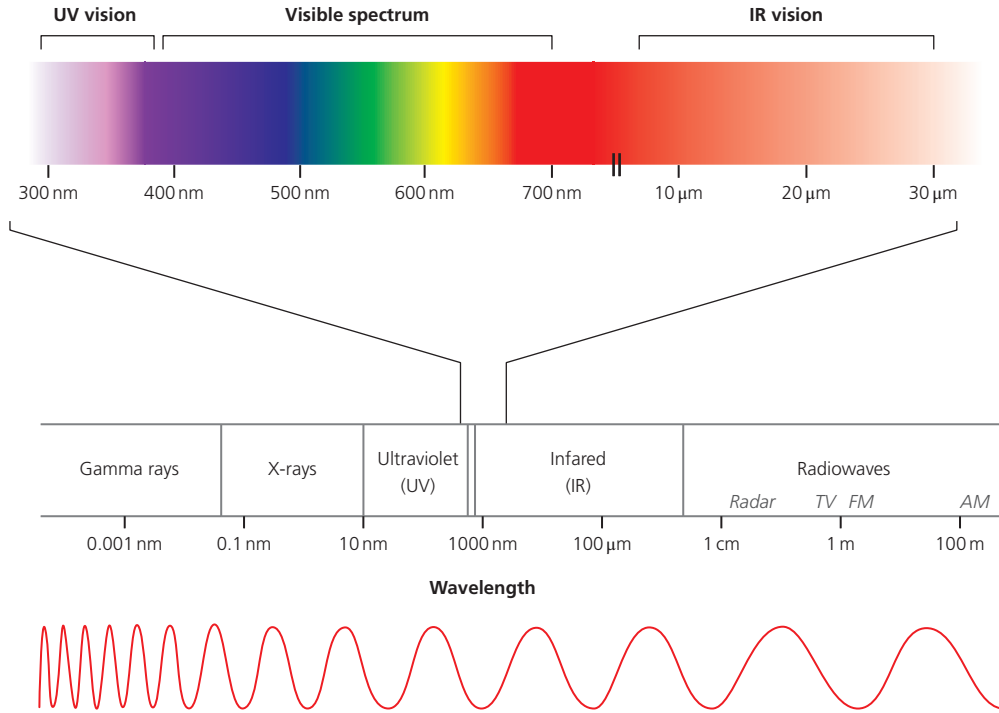


Figure 1.1 The electromagnetic (EM) spectrum. EM radiation spans a range of wavelengths, from low-energy, long wavelength radio waves to high-energy, short wavelength gamma rays. Most animals detect light only within a very narrow range of wavelengths; for example, the ‘visible spectrum’ in humans is between is about 390–700 nm. Some animals are also capable of detecting ultraviolet radiation (insects, birds and fish) and infrared radiation (crotalid and boid snakes, fire-seeking beetles and vampire bats).

possess a trichromatic visual pigment system. The **cone cells** of the human retina contain photo-pigments that absorb either red, green or blue wavelengths of light that has bounced off objects² in the environment, and our brains then interpret the mixtures of cone signals as different colours. However, cones have a relatively high response threshold, and thus only respond if the light is quite bright. We possess an additional set of photoreceptors, the **rod cells**, which absorb light across the full visible spectrum and, thus, are unable to distinguish between different colours, but are very sensitive to low light levels. The rod system therefore only mediates greyscale imaging (and the rod pigments are completely bleached in bright daylight), but it can function at low ambient light levels, in which the cone system is effectively blind. The two systems overlap and operate in parallel at intermediate light levels, such as twilight. Not all animals possess colour vision but, for those

²Object colour is often due to the extent to which some wavelengths of light are absorbed and others reflected off the object. For example, blue paint appears that colour to us, because the paint absorbs all visible wavelengths except ‘blue’, which is reflected back to the observer. If the observer has a photo-pigment which *absorbs* blue, then the blue light energy is converted into nerve activity, and the observer sees the object as blue. If, however, the observer does not have a pigment that absorbs blue, then the object appears black, and can only be detected in contrast to surrounding objects for which the observer *does* have a pigment capable of absorbing reflected light.

that do, it can be very useful in detecting warning coloration, such as aposematic beetles that warn predators they are distasteful.

Many animals are able to detect wavelengths of light beyond the spectrum to which humans are restricted (Figure 1.1). For example, many insects, birds and fish can visualise shorter wavelengths of light in the **ultraviolet** (UV) range, and they do so to detect a range of important ecological features, from enticing landing strips on flowers (bees) to the detection of aerial insect prey against the sky (dragonflies)³. One of the few mammals that can see in UV is the arctic reindeer (caribou), and here the key advantage seems to be contrast enhancement (Hogg *et al.*, 2011). The ground is often snow-covered, and predators such as wolves, with white fur, are hard to detect in the normal visible spectrum. However, snow is a strong reflector of UV, while fur is a strong absorber, which means that, in the UV spectrum, the wolf stands out clearly against a snowy background.

At the other end of the spectrum, some animals can also detect light in the longer wavelength **infrared** (IR) range (see Campbell *et al.* (2002) for a general review). Fire-seeking beetles, for instance, can detect IR light emitted by forest fires at a distance of up to 80 km, allowing them to navigate to freshly burnt wood, into which they lay their eggs (Schmitz and Bleckmann, 1998). Vampire bats possess IR-detecting receptors on their facial nose-leaf that are used to locate the most nutritious, blood-rich regions of a target prey animal. However, the most sophisticated IR visual system belongs to crotalid and boid snakes, which includes pit vipers, boas and pythons. These snakes possess highly specialised IR-detecting organs on their snout which allow them to detect, locate and capture their warm-blooded prey, even in what we would consider to be the dark (see Section 1.5).

Many animals, including a number of arthropods and cephalopods, are also highly sensitive to another property of light: **polarisation**. Mantis shrimp are the most sensitive – they have 12 visual pigments, and not only can they detect UV and IR radiation, but also circularly and linearly polarised light! Polarisation sensitivity is probably mainly used for navigation, but it can also be used for detecting certain types of prey – for instance, squid use polarized light sensitivity to visualise otherwise invisible, transparent zooplankton (Shashar *et al.*, 1998).

1.2 Eyes: acuity and sensitivity

The quality of an eye and, therefore, its usefulness to either predator or prey, strongly depends on two key factors:

- **Sensitivity** – the amount of light energy that it can capture from a given source.
- **Resolution (acuity)** – the accuracy with which it can determine the spatial origin of that source.

Sensitivity depends partly on receptor physiology, but also on eye structure. Basically, eyes with large lenses can focus more energy from a given point onto a receptor than eyes with small lenses⁴. Resolution depends on how well the optics can bring a point in the real

³Ultraviolet vision was first observed in the late 19th century by Sir John Lubbock, who discovered that ants could see in UV. He was a friend and neighbour of Charles Darwin.

⁴The biggest eyes in the animal kingdom, up to 25 cm in diameter, are found in giant squid. The squid live at such great depths that there is virtually no sunlight penetration, and the main purpose of the giant eyes may be to detect the early-warning bioluminescence generated by plankton which have been disturbed by the approach of one of the squid's deadly predators, the sperm whale.

world into focus as a point on the receptor surface, as well as the ‘pixel density’ of the receptors on that surface. Some photoreceptors are so exquisitely sensitive that they produce a detectable response to the capture of a single photon but, to gain useful information about the quality of the light source, many photons have to be captured – and the more photons per second the eye can direct onto the receptor, the quicker and more accurately the animal can analyse the image and produce a useful response.

There is an inevitable trade-off between resolution and sensitivity. An eye could achieve excellent sensitivity by having large receptors at low density. Each receptor would then capture photons from a wide angle of visual space but, unfortunately, such an eye would have poor resolution, because it would not be able to tell which particular part of that wide angle was the actual source of the light. The reverse is also true: a high receptor density necessarily means that each receptor gets a smaller share of the available light. The optimal compromise between these conflicting requirements depends on the function to which the eye is put, and this is a key factor driving eye diversification in evolution (Land and Nilsson, 2002).

The two main eye types that we are concerned with in this book are the single-lensed optical system of the vertebrate (and octopus) eye, and the multi-lensed compound eyes of arthropods and some other invertebrates. In both cases, the size of the lens ultimately limits both sensitivity and the capacity to resolve detail. This is especially the case for compound eyes, which are composed of many miniature eyes, called **ommatidia**. Each ommatidium views a different part of the visual field so that, in effect, each one represents a single pixel of the final image^{5,6}.

The acuity of an ommatidium ultimately depends on its ability to diffract light and this, in turn, is dependent on the diameter – the bigger the facet size, the better its diffraction power and the better the image. However, the trade-off is that fewer big facets can be accommodated for a given eye size. In fact, to achieve the resolution achieved by the human eye, a compound eye composed of standard-sized ommatidia would need to be approximately one metre in diameter!

1.2.1 Foveae

Acuity is not necessarily uniform across the whole visual field. Many animals have **foveae** in their eyes, which are regions with a particularly high receptor density and, therefore, where acuity is at its best. Foveal structure depends on the visual ecology of the animal concerned. Animals for which most objects of interest occur on a one-dimensional horizontal line tend to have a broad **visual streak fovea** (also known as an **infula**), which gives them a horizontal field of best vision of more than 100°. This includes grassland herbivores such as antelopes, gerbils or rabbits (Heffner and Heffner, 1992), and high-speed open-terrain predators such as cheetahs and wolves (Peichl, 1992; Ahnelt *et al.*, 2006). In contrast,

⁵This is true for apposition compound eyes. Superposition compound eyes can gather light across many ommatidia and focus it through a **clear zone** onto a receptor surface, rather like the retina in a vertebrate eye. These eyes sacrifice acuity for sensitivity, and tend to be found in nocturnal insects such as moths. Some compound eyes can switch from superposition to apposition optics and back by migrating pigmented sheaths within the clear zone.

⁶If you view a compound eye carefully you can often see a small dark area, called a pseudopil, which appears to follow you as you move around the animal. This represents the region of the eye that is looking directly at you. It appears black because it is absorbing, rather than reflecting, the light that is reflected off you and into the eye.

animals that operate in a two dimensional (2D) visual environment, where the vertical is as important as the horizontal (such as most primates, or a rodent such as a rat), tend to have a single spot fovea in each eye, which gives them very good resolving power within a relatively narrow field⁷. Cats and other predatory felids (except for the cheetah mentioned above) have an intermediate fovea which is extended horizontally into an ellipsoidal shape, but which is still relatively restricted (Land and Nilsson, 2002).

Some animals have multiple foveae within their eyes. Birds of prey (raptors), such as the kestrel, have a forward-looking **shallow fovea** in each eye, which together provide binocular vision, while a lateral-looking **deep fovea** in each eye provides monocular vision on either side. These birds can thus potentially look at three objects at the same time – one straight ahead and one on either side (which is rather hard for us to imagine). When a perching raptor sees something interesting, it tends to flick its head between the three positions to fixate the object at each fovea in turn.

The two foveae within each raptor eye are connected by a visual streak, whose acuity is lower than either fovea, but which is still greater than that of the rest of the retina. The lateral foveae have exceptionally high acuity – more than twice that of the human fovea (which itself is pretty good) – and these are used for long-range (>40 m) detection and pursuit of prey. At this range, the binocularity of the shallow fovea would provide little extra information, due to the small eye separation of a kestrel, but the enhanced acuity of the deep fovea is crucial in enabling early detection of small prey.

A consequence of using the lateral fovea for prey fixation is that raptors often follow a spiral flight path when chasing their prey, since they need to keep the prey at an angle to their direction of flight (the alternative, of flying at speeds of up to 180 mph with their head turned sideways, would be aerodynamically unsatisfactory; Tucker, 2000). As the raptor catches up with its prey, the chase turns into a follow-on pursuit and, as this happens, the image slides along the visual streak and becomes fixated on the forward-directed fovea, which has binocular overlap with its contralateral homologue. This means that at close range (<8 m), the stereopsis of the forward foveae provides good range information, which is presumably advantageous in the final stages of the hunt (Schwab and Maggs, 2004).

Exactly the same technique is used by kingfishers (Campbell, 1971). These birds also have two foveae in each eye, and they use the high-acuity monocular fovea, which is positioned nasally, to search for fish as the birds hover above the water. Once a fish is identified, the kingfisher plunges below the surface of the water, causing the fixation point to shift to the auxiliary forward-looking binocular foveae. Although these have fewer photoreceptors, and therefore produce a less sharp image than the main monocular foveae, the benefit of stereoscopic vision for detecting the three-dimensional movement of an escaping fish presumably outweighs this loss of acuity.

However, kingfishers have a further problem, not shared by raptors such as the kestrel – their underwater prey may not actually be where it appears to be from the search position! If the kingfisher views the water at an angle, then refraction at the air-water interface will bend the light, so that the fish will appear to be at a shallower depth than it actually is. The deeper the fish, the worse the distortion. Kingfishers seem to solve this problem by attacking deep prey with a steeper dive angle than shallower prey. If the kingfisher positions

⁷We ourselves have a single fovea in each eye, which gives us an excellent resolving power of about 1/60 of a degree of arc under ideal conditions, but this is only achieved over the central two degrees of vision.

itself directly overhead and dives vertically, then there will be no refraction shift at all, and the kingfisher can aim straight at the true location of its prey⁸.

1.3 Feature recognition and releasing behaviour

An appropriate response to the detection of a prey animal is usually very different from an appropriate response to a predator. It is therefore crucial that an animal can tell the difference! Many animals possess a feature recognition system that extracts important elements of incoming visual signals to compute object identity, and then relays this information to the motor system to coordinate an appropriate behavioural response (attack, escape or ignore). The combination of visual signals that release a particular behaviour – often called the **key visual stimuli** – includes not only the movement of an object, but also its *shape*, *form*, *speed* and *direction* of movement. The term derives from the idea that a particular combination of signal properties will unleash a fixed pattern of behavioural response, in a manner analogous to a key being able to unlock a door. This process must involve computation and filtering of the stimulus properties in brain circuits that function in what was termed an **innate releasing mechanism**.

In a series of classic experiments conducted by Konrad Lorenz and Nikolaas Tinbergen in 1937 (see Schleidt *et al.*, 2011 for a historical review), escape responses could be triggered in turkeys by the outline of a bird, so long as the *direction* of its movement indicated that the bird was a hawk (Figure 1.2). When an identical shape was presented, but moved in the opposite direction (so that it now resembled a goose), the turkeys did not try to escape. Interestingly, this escape response is gradually refined during development; young turkeys respond to aerial threats, regardless of shape and direction, but adults learn that geese are innocuous, while hawks are a potential threat (Tinbergen, 1948, 1969).

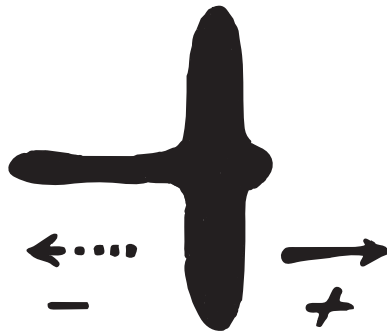


Figure 1.2 An innate releasing mechanism in turkeys. The presentation of a simple cardboard dummy of a bird moving in the direction to the right is recognised by turkeys as a threat (a ‘hawk’), and initiates escape behaviours such as alarm calling and avoidance. However, if the exact same visual stimulus is flown to the left, the stimulus is perceived as non-threat (a ‘goose’) and is ignored. Tinbergen (1969), originally published in 1951. Reproduced by permission of Oxford University Press.

⁸We will see in a later chapter how a predator acting in the reverse direction has come up with a different solution to the same problem. Archer fish attack airborne prey from an underwater viewpoint, and they simply adjust their aim to take account of the diffraction at the water-air interface (Chapter 10, The Ballistic Attack of Archer Fish).

1.4 Prey capture in toads

Many animals display fixed, stereotyped behaviours when presented with particular visual stimuli. For instance, male sticklebacks reliably and aggressively attack almost any object whose lower half has been coloured red, which mimics the red belly of a rival male during the breeding season (Tinbergen, 1952)⁹. The common toad (*Bufo bufo*) is another example and is an important model in neuroethology, as it was one of the first vertebrates used to bridge the gap in understanding between neurons and behaviour. In particular, it has been used extensively to examine the relationship between properties of a visual stimulus and the recognition of that object as predator or prey.

The visual system of the toad differs from ours in a number of ways. When we look out onto the world, we produce small, rapid and involuntary movements of our eyes, known as **saccades**, which enable us to scan static visual scenes for salient information. In contrast, toad eyes are relatively fixed – they do not produce eye saccades and, as such, their visual system is thought to be effectively blind to static scenes (Ewert, 1980). It has even been stated that a toad ... ‘will starve to death surrounded by food if it is not moving’ (Lettvin *et al.*, 1959). The toad is interested in *moving* things, and this is reflected by a visual system tuned to respond to simple moving objects, such as a fly landing on a leaf, a worm crawling across the ground or a bird flying overhead. The prey-catching or predator-avoiding behaviours triggered by such stimuli perfectly illustrate the concept of an innate releasing mechanism.

1.4.1 Attack or avoid: ‘worms’ and ‘anti-worms’

The common toad is a classic ‘sit-and-wait’ predator – it will remain motionless for long periods of time, until an object of interest moves into its field of view. When the toad recognises a moving object as prey, such as a small insect or worm, it initiates a sequence of behaviours in which one action triggers the next to form a **stimulus-response chain**. Firstly, it will orient its head and body towards the prey, so that both eyes are fixed on the target and, if the prey happens to move out of view, the toad will reorient itself to maintain binocular fixation. Next, it will approach the prey and, once in reach, it will snap out its tongue and take the prey into its mouth. The toad will then gulp down its meal before finally performing a cartoon-like wipe of the mouth with one of its forelimbs. This sequence is highly stereotyped and, once triggered, usually plays through to the end; even if a pesky experimenter removes the prey mid-sequence, the toad will still approach, snap at where it thinks the prey should be, swallow, and then proceed to pointlessly wipe its mouth (Ewert, 1974).

Escape and avoidance behaviours are triggered by threatening stimuli, such as a large, looming object. These behaviours are often more variable than a prey capture sequence, and depend on the nature of the visual threat (e.g. ground predator vs. aerial predator), but they may include crouching defensively, standing up and inflating itself, or simply jumping out of the way (Ewert, 1980).

The above behavioural sequences can be reliably and repeatedly reproduced in a laboratory, using simplified shapes to mimic predators and prey. The neuroethologist Jörg-Peter Ewert conducted a series of experiments in which toads were placed inside a glass chamber on a circular table, and pieces of cardboard of varying size, shape and orientation were

⁹This response to red objects is so robust that Tinbergen observed that sticklebacks would even display the aggressive behaviour when red Royal Mail trucks passed by the laboratory window (Tinbergen, 1952).

presented to the toad on a rotating arm (Figure 1.3; Ewert, 1974, 1985, 1987). The degree to which a shape was recognised as prey could then be measured by the amount of orienting behaviour towards the stimulus.

If a small, horizontally-elongated shape was moved in the direction of its long axis, it was recognised as prey, and the toad showed clear orienting behaviour; this stimulus can be considered to have a **worm configuration** (Figure 1.3B)¹⁰. The more ‘worm-like’ the visual stimulus, the stronger the orienting response. If, on the other hand, the exact same shape was moved in the direction perpendicular to its long axis, it was either ignored or perceived as a predator (such as a snake), and met with avoidance or defensive behaviour; this stimulus has an **anti-worm configuration** (Figure 1.3A). The actual *direction* of movement doesn’t matter - for example a vertically-elongated shape moving upwards (i.e. still in the

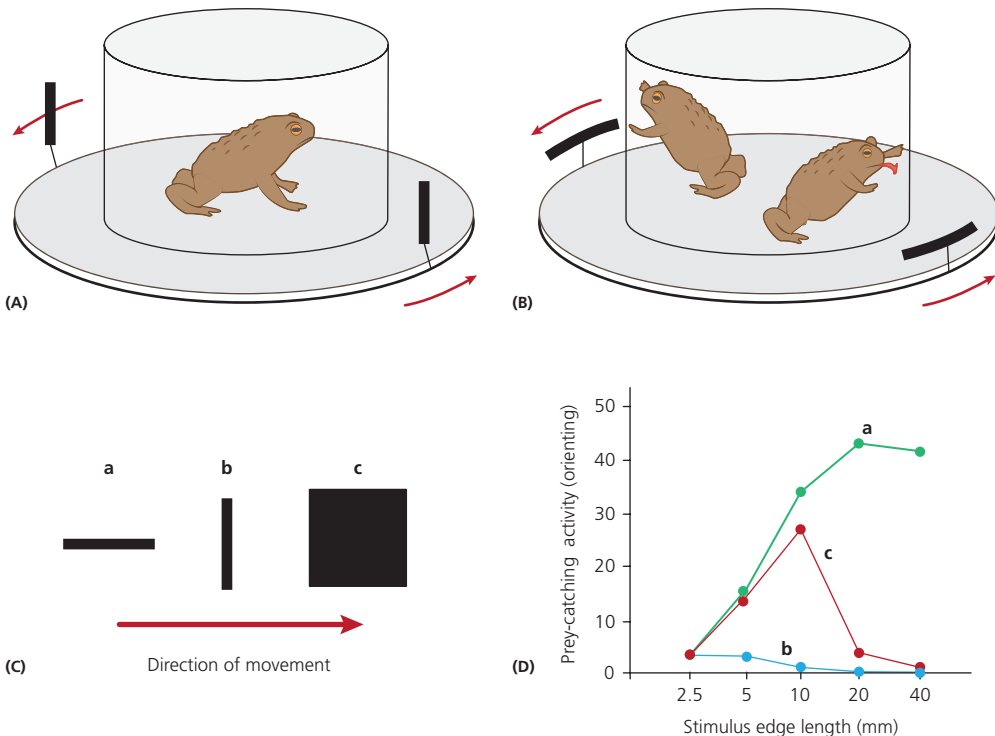


Figure 1.3 Behavioural responses of the common toad (*Bufo bufo*) to different moving shape configurations. **A:** A toad will not attack a rectangular bar moving in the direction perpendicular to its long axis. Such a stimulus is considered to have an ‘anti-worm configuration’. **B:** When the same exact shape is presented, but moving in the direction parallel to its long axis, it is recognised as prey and the toad prepares to attack. This stimulus is considered to have a ‘worm configuration’. **C:** Examples of the different types of stimulus shapes presented to the toad. **D:** Graph showing the effect of stimulus size on prey-catching behaviour. For shapes in the worm configuration (a in graph), the more elongated the bar, the stronger the orienting response. For anti-worm configurations (b in graph), orienting behaviour decreases as the bar gets longer, as the toad starts to show avoidance behaviour. For a square stimulus (c in graph), the size becomes very important. Small squares are perceived as prey, while larger squares are perceived as predator. C, D adapted with permission from Ewert (1985).

¹⁰Toads do not only eat worms, but most of their prey do fit the ‘worm configuration’ – small, elongated objects that move in the direction of their long axis, such as mealworms, slugs, millipedes and beetles.

worm configuration) is also considered prey by the toad, presumably mimicking prey climbing an object such as the trunk of a tree¹¹.

What are the neural mechanisms that underpin this predator-prey recognition system? It is clearly the shape and direction of movement with respect to stimulus orientation that determines whether a toad recognises a stimulus as prey. It follows that at some point in the visual pathway, there are neurons or groups of neurons that encode these sign stimuli – but at what level of the visual pathway do such prey **feature detectors** exist?

1.4.2 Retinal processing

The rods and cones are the primary photoreceptors that respond to light entering the toad's eye. Multiple photoreceptors pass signals onto a smaller number of bipolar cells, which themselves converge onto **ganglion** cells, of which there are around half a million in the visual system of the toad. Additional lateral connections from horizontal and amacrine cells are also present, and modify the neural signals being transmitted to the ganglion cells. The ganglion cells are the only neurons that actually leave the retina and carry the visual signal to the brain¹², but the circuitry of the retina means that there is a considerable amount of pre-processing of visual information before any signal reaches the brain.

Each ganglion cell has a **receptive field** defined by the region of the visual field to which it responds. **On** cells are excited by an increase in illumination at the centre of their receptive field, while **off** cells are excited by a decrease. **On-off** cells are excited by a change in either direction. Furthermore, most ganglion cells show a **centre-surround** response property, which means that they are excited by an appropriate stimulus in the centre of their receptive field, but inhibited by the same stimulus in the periphery of the field. Such neurons are thus particularly responsive to spot or edge stimuli. There are further specialisations amongst ganglion cells in terms of their preference for moving versus stationary objects, the size of their receptive fields, their axonal conduction velocity, and various other features.

In 1959, Jerry Lettvin and colleagues¹³ published a landmark study entitled 'What the frog's eye tells the frog's brain'¹⁴. The key message in this article was that the ganglion cells are not just *relaying* visual information to the brain but are, to a certain extent, *interpreting* it as well. Thus ganglion cells which responded to a small moving spot irrespective of features in a stationary background were thought of as 'bug perceivers' (although formally described as convexity detectors), while off-cells with large receptive fields which were particularly sensitive to dark, looming stimuli were thought to be ideal candidates for detecting a predator. Subsequent experiments have failed to find toad ganglion cells that can clearly differentiate between predator and prey stimulus configurations (Ewert, 1997) but, nevertheless, the Lettvin results sparked the concept that individual neurons can act like feature detectors, and this has proved to be enormously influential.

¹¹Other shapes, such as squares, were also presented to the toad. For square stimuli, the size of the stimulus was important – small square stimuli tended to be perceived as prey, and elicited orienting behaviours, whereas larger squares were perceived as predators and induced avoidance responses.

¹²The retina is derived from the neural tube and so, embryologically speaking, it is actually *part* of the brain. However, its anatomical separation makes it convenient to regard it as a separate unit.

¹³The colleagues included Warren McCulloch and Walter Pitts, two of the pioneer researchers in artificial intelligence and neural network theory.

¹⁴Jerry Lettvin had a way with words – he later coined the term 'grandmother cell' to describe an individual neuron whose activity corresponds to a highly complex and meaningful stimulus, such as the sight or sound (or smell) of one's grandmother. Whether such neurons actually exist is still a matter of considerable debate, but the phrase undoubtedly captures the essence of a key hypothetical mechanism for feature recognition.

1.4.3 Feature detector neurons

Visual information from the retina passes through the optic nerve to the brain¹⁵, where there are two main areas involved in feature recognition – the **optic tectum** and the **thalamic pre-tectal** area (Figure 1.4). Both areas contain a **topographic map**¹⁶ of visual space, containing a range of visually sensitive neuron classes.

In the optic tectum, there are nine classes of neuron (T1–T9), and microelectrode recordings by Ewert and colleagues revealed that two subtypes, T5.1 and T5.2, play a particularly important role in signalling prey feature recognition. T5.1 cells receive excitatory input from ‘bug perceiver’ and on-off retinal ganglion cells and fire strongly when the toad is presented with prey stimuli (worm shapes and small squares), but ignore threatening stimuli (anti-worm shapes and large squares; Figure 1.4, left). These T5.1 cells provide excitatory input to the second important subtype, T5.2 cells, which again fire strongly to prey stimuli, but also decrease their firing rate in response to threatening stimuli (Figure 1.4, left).

Thus, the firing pattern of T5.2 cells distinguishes between worm and anti-worm shape configurations, and can perhaps be considered the elusive ‘prey-detector’ neurons that

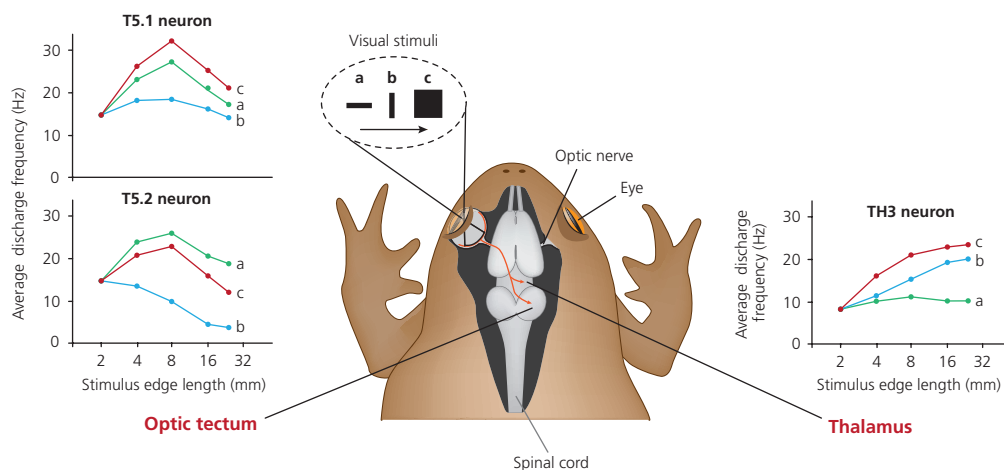


Figure 1.4 The visual pathway of the toad, and stimulus-response properties of tectal and pretectal neuron subtypes. Middle: Light is transduced at the retina by photoreceptors, and retinal ganglion cells project via the optic nerve to the contralateral optic tectum and thalamic pretectal area. Left: Neuron subtypes in the optic tectum show a preference for prey-like stimuli. T5.1 cells (top graph) increase their firing rate to small moving squares and horizontal bars, but are relatively unaffected by stimuli in the non-prey configuration. T5.2 cells (bottom graph) are also excited by prey-like stimuli, but reduce their firing rate to non-prey stimuli (large moving squares and vertical bars). Right: Cells in the thalamus show a preference for non-prey stimuli. TH3 cells increase their firing rate to large squares or vertical bars, but are unaffected by prey-like stimuli. Graphs adapted from Ewert (1985).

¹⁵Note that in the toad visual system, information from one eye passes completely to the contralateral side of the brain, which is unlike humans and other mammals, where there is only partial decussation of the optic nerve.

¹⁶A topographic map is formed when there is an ordered 1 : 1 correspondence between some spatial location in the real world and a spatial location within a neural array. The ordering is arranged so that adjacent regions in the real world correspond to adjacent regions in the neural array, and the array thus forms a map of the real world.

were once proclaimed to exist at the level of the toad retina. The importance of this tectal pathway for prey recognition was demonstrated by artificially activating T5.1 or T5.2 cells in freely moving toads, using surgically implanted electrodes. The results were strikingly clear – activation of either T5.1 or T5.2 neurons triggered attack behaviours, including orienting, snapping and the characteristic mouth wiping (Ewert, 1974). Moreover, this orienting and snapping was directed specifically towards the region of real space corresponding to the site of the stimulated tectal region, demonstrating the role of this pathway for prey localisation, as well as recognition.

The second important brain area, the thalamic pretectal area, receives input mainly from ‘on-off’ and ‘off’ ganglion cells, and contains various neuron subtypes (TH1–TH11) responsive to predator-related visual stimuli, such as large, looming objects or horizontal bars in the anti-worm configuration. One subtype, TH3 neurons, was especially sensitive to the large squares and anti-worm shapes used in the behavioural studies (Figure 1.4, right). Activation of these TH3 neurons using electrode implant stimulation reliably produced avoidance behaviours, such as ducking, closing eyelids, or turning away from the region in space corresponding to the stimulated region of thalamus. Thalamic TH3 neurons therefore play an important role in recognising threatening stimuli and initiating escape and avoidance behaviours.

Ewert and colleagues discovered that TH3 neurons play a further important role in the toad’s brain. Numerous experiments provided strong evidence for inhibitory connections from the TH3 neurons to the T5.2 neurons, thus sharpening the specificity of the worm-detecting properties of the latter. For instance, if the thalamic pretectal area is electrically stimulated at the same time that a prey stimulus is presented to the toad, inhibition overrides the normal excitatory responses of T5.2 cells and prevents the associated attack behaviours. Conversely, if the connections from the thalamic pretectal area are removed (using micro-surgery or anaesthesia) it results in clear *disinhibition* of the prey signalling pathways, at both the cellular and behavioural level. The T5.2 tectal cells in these lesioned animals show increased firing, and can no longer distinguish worm and anti-worm shapes.

Behaviourally, these disinhibited toads orient towards and attack almost any moving stimulus presented, regardless of its identity as predator or prey – tested stimuli included a shoebox, an experimenter’s hand, another toad, and even the toad’s own legs (as long as they were moving), all of which were snapped at as if recognised as viable prey (Ewert, 1985). The inhibitory connections from the thalamus to the T5.2 cells in the optic tectum therefore appear to be fundamental not only to the recognition of threatening stimuli and the initiation of avoidance behaviours, but also to the accompanying suppression of attack behaviour. The inhibitory effects of the thalamic pre-tectal area appear to be mediated by Neuropeptide Y, which is released within the optic tectum, and results in pre-synaptic inhibition and a subsequent reduction in glutamate release by tectal neurons (Ewert and Schwippert, 2006).

The predator-prey feature recognition system in the toad was one of the first case studies in neuroethology, in which a simple vertebrate behaviour was traced to the activity of identified groups of neurons. In the toad brain, there exist two parallel pathways – one excited by prey visual stimuli (the retino-tectal pathway), and the other by non-prey stimuli (the retinopretecto-tectal pathway), which converge onto T5.2 cells of the optic tectum. Here, the balance between the excitatory influence of the prey pathway and the inhibitory influence of the predator pathway ultimately determines whether a signal is sent to the motor system to initiate a prey capture sequence (Figure 1.5).

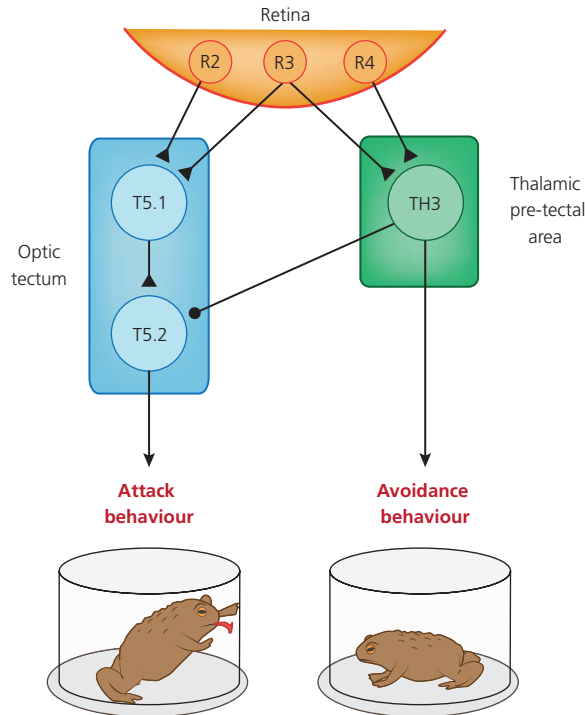


Figure 1.5 A simplified model for the parallel and converging pathways involved in visual predation in toads. Prey stimuli, such as small squares or shapes in the worm configuration, will selectively activate R2 ('bug perceiver') and R3 (on-off) retinal cell types, to excite T5.1 cells in the optic tectum. T5.1 cells relay this excitation onto T5.2 cells, which send signals to the bulbar/spinal systems to initiate attack behaviours. Conversely, non-prey and threatening stimuli, such as anti-worm shapes and large squares, will selectively activate R3 and R4 (off) retinal cells, which activate TH3 cells in the thalamic pre-tectal area. TH3 cells inhibit the T5.2 cells, inhibiting attack sequences and allowing the initiation of escape and avoidance behaviours.

1.4.4 Modulation and plasticity

Innate releasing mechanisms, such as the prey capture sequence in toads, were traditionally viewed as being fixed throughout development and across different environmental conditions (Ewert and Schwippert, 2006). The neuronal network responsible for recognising predators and prey appears to be relatively hard-wired inasmuch as it is present in young toads shortly after metamorphosis. However, the configurational selectivity does increase during development, as toads become more experienced in prey selection. Moreover, the network is influenced by the activity of various forebrain structures involved in attention and motivation, which have been shown to be important in controlling features of the recognition system, such as stimulus discrimination, habituation and hesitation (Ewert *et al.*, 2001; Ewert and Schwippert, 2006). The response to a visual stimulus can also be conditioned. For example, an untrained toad will normally show avoidance behaviour to an experimenter's hand but, if the hand contains a worm, it will recognise the prey and snap at it, despite the hand being present. If repeated, the toad eventually becomes conditioned to snap at the hand, even if it no longer contains a worm. The conditioning process is thought to involve a reduction in the activation of the thalamic pretectal area, so that the tectum becomes disinhibited (Ewert and Schwippert, 2006).

1.4.5 Toad prey capture: the insects fight back

The innate releasing mechanism of anurans unleashes an all-or-nothing behavioural response that has evolved to facilitate prey capture. In one remarkable twist of fate, however, the tables are turned and the prey becomes the predator. Beetle larvae certainly appear like tasty morsels to frogs – indeed, their shape and direction of movement fits the ‘worm configuration’ – but beetle larvae of the genus *Epomis* take advantage of the predictability of the frog and toad behaviour to strike back and predate upon their amphibian opponents (Figure 1.6; Wizen and Gasith, 2011).

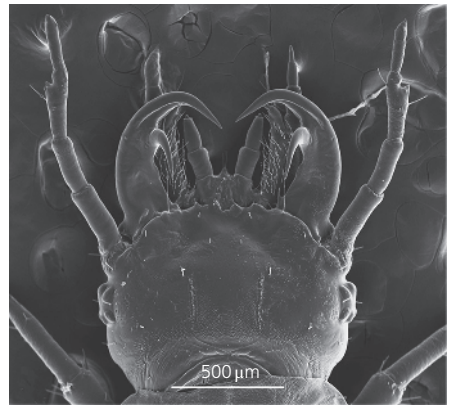
In fact, these *Epomis* larvae feed exclusively on juvenile and adult amphibians. They deliberately induce a predatory strike from the amphibian by waving their antennae to draw attention to themselves but, because they know what’s coming, they are usually able to evade the predatory strike. They then strike back immediately while the amphibian is within close range, firmly locking onto the amphibian’s skin surface using a pair of unique, double-hooked mandibles (Figure 1.6B). Once attached, the larva sucks the bodily fluids from the anuran. This parasitic-like feeding often progresses to chewing and eating the body tissues, eventually resulting in the toad’s death.

Even if the amphibian does manage to capture the larvae with its initial strike, it does not necessarily result in a good outcome for the toad or frog. In one case captured on film, a young frog captured the beetle larva in its mouth, but did not seem to enjoy the experience. After repeated attempts to eject it, the young frog eventually swallowed the larva whole. Two hours later it regurgitated it; the larva was covered in mucus, but otherwise appeared unharmed. Eventually, the larva triggered the frog to strike again but, when it came within striking distance once more, the larva spun around and latched onto the skin, to restart the predation sequence.

The only pause in the proceedings of larval predation of anurans comes when the larva moults. At this stage, the larva drops off the host but, once the moult is complete, it seeks a new amphibian on which to predate. The adult beetle never loses its appetite for amphibians but, unlike the preceding larval stages that feed exclusively upon frogs and toads, the dietary range increases.



(A)



(B)

Figure 1.6 The *Epomis* ground beetle lures anurans by exploiting their innate attack response towards small moving objects. **A:** A green toad attacked a beetle larva (*Epomis circumscriptus*), but the larva has latched on to the toad’s tongue. It will now begin to eat the toad. **B:** An SEM of the head of a ground beetle larva (*Epomis dejeani*) shows the specialised double-hook mandibles used to lock onto the skin surface of toads. From Wizen and Gasith (2011), CC-BY licence.

1.5 Beyond the visible spectrum

In the 1987 film, *Predator*, starring Arnold Schwarzenegger, a team of Special Forces soldiers is stalked by an advanced alien species. Despite being outnumbered, outmuscled and outgunned the Predator picks off the commandos one by one because it has a key sensory advantage over its prey – **infrared vision** – enabling it to ambush the warm-blooded soldiers while remaining invisible in the dark jungle environment. True infrared vision (or thermal vision) is not purely a work of fiction but has evolved in a number of species of boid snakes (including pythons and boas), and independently in the distantly related crotalid snakes (pit vipers). In addition to their normal vision, these snakes produce a thermal image of their environment that allows them to target warm-blooded prey with remarkable accuracy, even in the conditions of low light levels favoured by these ambush predators. Their infrared vision is not a distinct so-called ‘sixth sense’ but is, instead, highly integrated into the snake’s normal visual system, and overlaps to produce what is thought to be a single, coherent visual representation of the world.

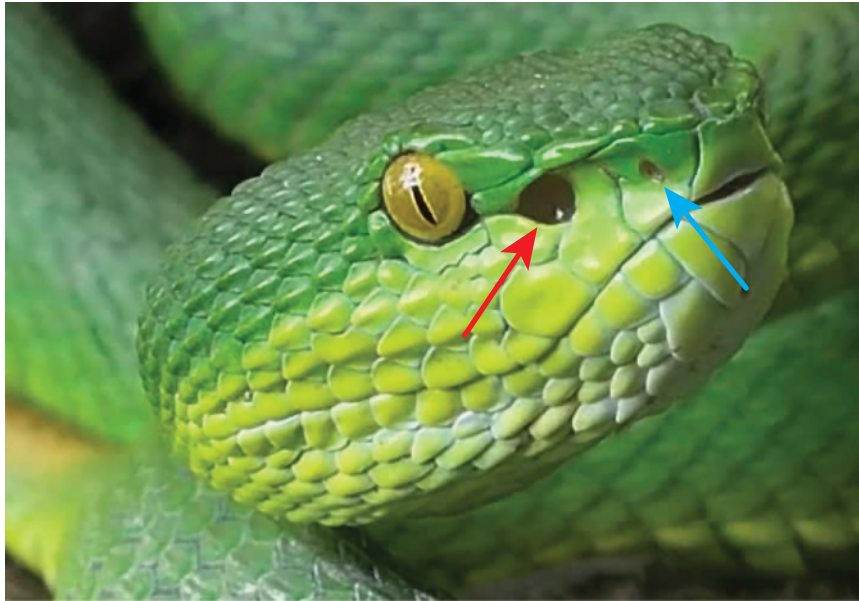
1.5.1 Pit organs

Infrared radiation spans from the red end of the visible spectrum (700 nm) to the start of the microwaves (1 mm), but snakes have detectors that work in the 5–30 μm range (Figure 1.1). The sensors are small, forward-facing cavities on the head, known as **pit organs** (Figure 1.7) which were first shown to be sensitive to IR radiation in the 1930s (Noble and Schmidt, 1937). Pit vipers possess a single pit organ (also known as a loreal pit), around 1–5 mm in diameter, on either side of the head between the eye and nostril. Stretched across the inner chamber of each of these small cavities is a thin, suspended membrane ($\approx 15 \mu\text{m}$ thick) that acts like a kind of thermal ‘eardrum’. The membrane has an inner and outer epithelial layer, and the region lying between them is densely innervated by thermosensitive trigeminal nerve endings, known as **terminal nerve masses** (TNMs)¹⁷. These nerve endings are the IR detectors, and they carry thermal information from the pit membrane to the optic tectum, where an IR map of space is generated.

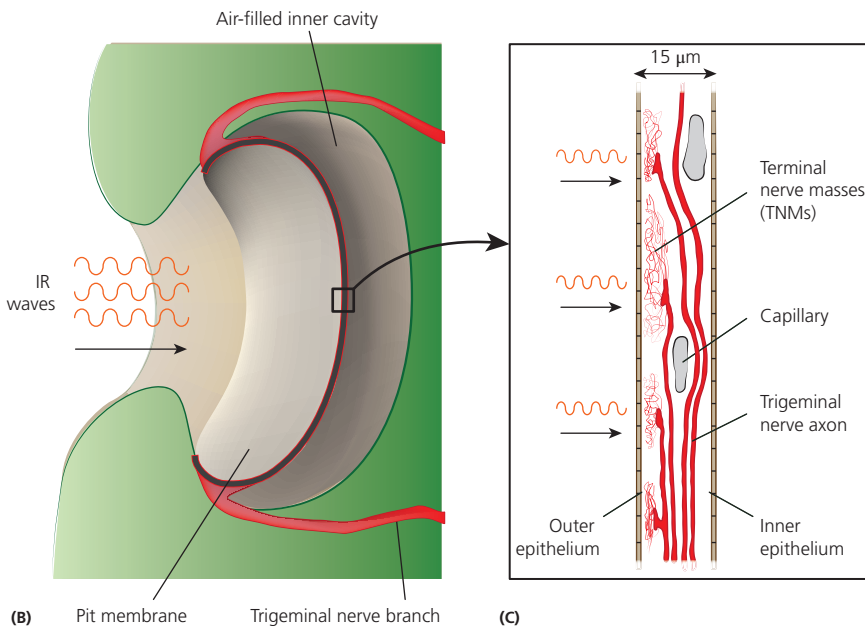
The pit organ functions like a **pinhole camera** – the organ has no actual lens, but the entry hole into the cavity focuses electromagnetic waves onto the highly sensitive and innervated membrane. This forms a 2D map of incoming IR information analogous to that of visible light on the retina, with a field of view of around 100 degrees (Newman and Hartline, 1982; Bakken and Krochmal, 2007). However, the projected thermal image is very blurred compared with normal vision (Figure 1.8), because the diameter of the pinhole is about 1 mm, which is too large to form a high-quality image¹⁸. This is a little surprising, because it is known from behavioural studies that thermal vision in snakes is actually very detailed and accurate, and can compensate well for the loss of normal vision in a blind snake (see Section 1.5.4 below).

¹⁷In boid snakes the pit organs occur as clusters of 3 or more cavities on the snout. The organs are known as labial pits and are less specialised than those of the pit vipers. For example the pit membrane is not suspended but instead lies at the bottom of the pit cavity, and is innervated by fewer nerve endings – as a result, the boid pit organs are around 5–10 times less sensitive to IR than those of the pit vipers.

¹⁸For optimal image quality, the pinhole diameter (d) should be about 0.25 mm ($d = \sqrt{2f\lambda}$, assuming a focal length f of 1 mm and IR wavelength λ of 30 μm ; Rayleigh, 1891). The larger actual size of the opening to the pit organ is probably due to an evolutionary trade-off between the need to optimise the image quality and the need to capture IR energy at a sufficient rate that moving prey can be detected in real time.



(A)



(B)

(C)

Figure 1.7 The infrared-sensitive pit organ of snakes. **A:** Photograph of a red-tailed bamboo pit viper (*Trimeresurus erythrurus*) showing the thermosensitive pit organ (red arrow). The nostril (blue arrow) is also visible. Photograph: Steve Kharmawphlang, Flickr, CC-BY-2 licence. **B:** A drawing of the pit organ. Infrared radiation enters the organ through an entry hole and hits a suspended membrane. The suspension of the membrane creates an inner cavity of air that prevents the unwanted absorption of radiation into the head tissue. **C:** The pit organ membrane is composed of trigeminal nerve endings sandwiched between two layers of epithelial cells. These nerve endings, called terminal nerve masses (TNMs), are sensitive to infrared radiation. The membrane is also densely infiltrated by a capillary network, which ensures the rapid removal of heat from the membrane. B, C adapted from Newman and Hartline (1982).

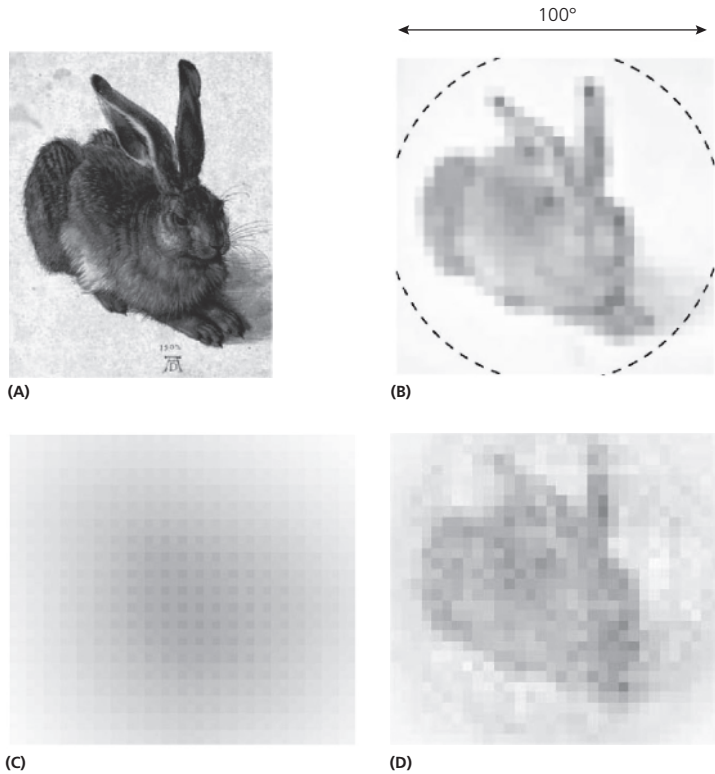


Figure 1.8 De-blurring a pinhole camera image through a plausible neural filter mechanism. **A:** Dürer's 1502 painting of a hare. **B:** The image of the hare was converted into 8-bit grey levels at a 32×32 resolution, with the grey level assumed to represent variations in body temperature. **C:** The predicted heat distribution on the pit organ membrane after projecting the image in B through the pinhole lens, sampled at 41×41 pixel resolution. The image is badly blurred as a result of a large aperture. **D:** The final image produced after de-blurring the image in C, using image-processing software implementing an algorithm resembling a Wiener filter. Adapted from Sichert *et al.* (2006), with permission from the American Physical Society.

There are up to 7000 thermosensitive axon endings distributed throughout the membrane of each pit organ, and these provide enough information to enable signal-processing circuitry in the medulla of the hindbrain to de-blur the image (Newman and Hartline, 1982; Moon, 2011). Theoretical studies suggest that relatively simple and neuronally-plausible algorithms can produce a final thermal map that would certainly be sharp enough to enable a snake to determine the location of a heat source, and probably sharp enough to allow it to determine the identity of the source, too (Figure 1.8; Sichert *et al.*, 2006).

Specialisations of the pit organ

The pit organ membrane is sensitive to thermal changes in the environment as small as $0.001\text{--}0.003^\circ\text{C}$ (Bullock and Diecke, 1956), and various specialisations of the pit organ itself contribute to this remarkably high sensitivity. Firstly, the TNM endings are extremely close ($<15\text{ }\mu\text{m}$) to the surface of the outward-facing side of the membrane. This makes them a lot more sensitive to small temperature changes than if they were more deeply embedded in tissue. Mammalian thermoreceptors are typically found around $300\text{ }\mu\text{m}$ deep in tissue, and this takes around 20 times more thermal energy to warm than tissue that is

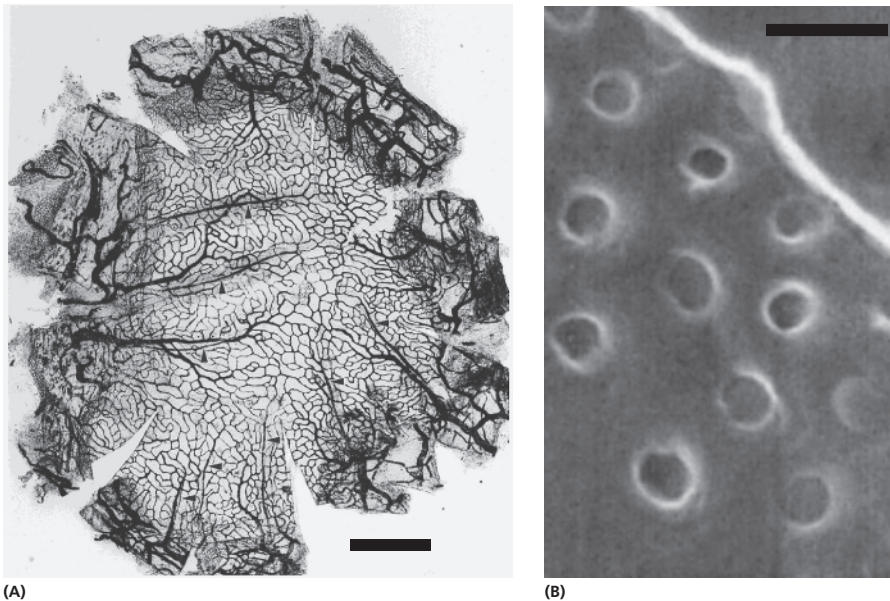


Figure 1.9 The pit organ capillary network and membrane surface ultrastructure. **A:** Whole mount of a pit organ membrane after staining of the capillary network using India ink. Slits have been made around the edges to allow the concave membrane to lie flat. Arrow heads show arterioles. Scale bar = 500 μ m. Adapted from Amemiya *et al.* (1999); reproduced with permission from John Wiley and Sons. **B:** Scanning electron microscope image of the pit organ membrane, showing micropits on the surface which help to filter out visible and UV radiation and enhance IR radiation absorption. Scale bar = 600 nm. Adapted from Campbell *et al.* (1999); reproduced with permission from Elsevier.

only 15 μ m deep (Newman and Hartline, 1982). Another specialisation is the physical suspension of the organ membrane itself. This creates an important pocket of air between the pit membrane and the snake's head (see 'inner chamber', Figure 1.7) and, since air is a good insulator, this prevents the unwanted loss of IR energy through tissue absorption.

Arguably the most important specialisation of the pit organ membrane is the presence of an extensive capillary network surrounding the TNMs, which acts as an effective **heat exchanger** (Figure 1.9A). This is essential for the function of the pit organ. If the membrane and nerve masses were to retain their heat, it would create a kind of 'after-image' in the snake's brain, similar to what would happen if our eyes were unable to refresh and update our visual representation of the world, but instead got stuck on a single still image.

The capillary network thus allows thermal energy to be carried away quickly from the pit organ, in order to ensure that it remains sensitive to real-time changes in the thermal environment (Amemiya *et al.*, 1999). Instead of maintaining a continuously high blood flow, which would be energetically costly, the capillary network upregulates local blood flow in response to real-time increases in IR radiation. These changes in blood flow are extremely fast (1–5 ms onset), are very local, and are proportional to the strength of the IR signal (Goris *et al.*, 2000, 2007). The mechanism is not fully understood, but is thought to involve the direct IR-mediated release of nitric oxide (NO) from trigeminal nerve endings. NO has potent vasodilator properties, and is thought to induce a surge of the intracellular second messenger cyclic GMP in a set of contractile cells called pericytes, leading ultimately to the rapid and local relaxation of smooth muscle at active regions of the pit membrane (Goris *et al.*, 2007).

An efficient heat exchange system is not the only specialisation that helps keep the pit organ membrane ‘thermally refreshed’. The surface of the pit organ itself is covered in arrays of even smaller pits, known as **nanopits** or **micropits** (Figure 1.9 B), which are typically around 300 nm in diameter and 46 nm in depth (Campbell *et al.*, 1999). The average spacing between these nanopit arrays is around 800 nm, and this is thought to provide grating spacing that efficiently reflects or scatters radiation in the visible and UV regions of the EM spectrum, thereby enhancing the selective absorption of IR waves. Thus, it has been suggested that the ultrastructure of the pit organ surface may function as a spectral filter of unwanted wavelengths of EM radiation, protecting the organ from non-infrared thermoreceptor heating that would otherwise contaminate the sensory signal (Campbell *et al.*, 1999; Fuchigami *et al.*, 2001).

1.5.2 Thermotransduction

Unlike normal vision, where light is transduced through a photoisomerisation process in separate specialised sensory cells (photoreceptors), the embedded terminal endings of the trigeminal nerve fibres themselves act as the sensory receptors for IR vision. The pit organs were known to be IR sensors as early as 1937, but it was not until the 1950s that the renowned neuroethologist Theodore Bullock and co-workers made the first electrophysiological recordings from these neurons (Bullock and Diecke, 1956).

In the absence of environmental changes, TNMs were found to exhibit continual non-rhythmic firing as a result of background IR radiation (Figure 1.10). Any increase in the level of IR resulted in a rapid increase in the firing rate of these nerve fibres, with a response onset of less than 100 ms. If the IR stimulus was sustained, the firing rate gradually dropped back down to baseline and, when the stimulus was then removed, the firing rate dropped below background level, before slowly recovering back to the pre-stimulus firing rate. A decrease in IR (relative to background) resulted in a reduction in the firing rate, even potentially silencing nerve fibres, accompanied by a similar pattern of adaptation if the stimulus was sustained.

The molecular mechanism underlying the IR transduction process remained a mystery until only recently. Gracheva and colleagues (2010) discovered that a particular protein was



Figure 1.10 TNM receptors in the pit organ adapt following stimulation. Prior to a stimulus, the TNM fibres fire spontaneously as a result of background infrared radiation. An increase in infrared radiation (top) causes an increase in the TNM fibre firing rate. If the stimulus is sustained, the firing rate gradually drops, due to desensitisation. When the stimulus is then removed, the firing rate drops below the baseline rate, before slowly recovering. The opposite happens if background radiation is reduced (lower). Adapted from Newman and Hartline (1982).

highly enriched (by 400-fold) within the trigeminal ganglia of thermosensitive snake species, compared with those that lack thermal vision. The protein is a cation-selective ion channel called **transient receptor potential Ankyrin 1** (TRPA1), a member of the TRP family of receptors involved in sensations such as nociception, temperature, taste and pressure. This makes a lot of sense, because the thermoreception pathway is part of the somatosensory system.

In humans, the equivalent of TRPA1 is known as the **wasabi receptor**, which is responsible for the painful burning sensation following contact with chemical irritants such as mustard oil and wasabi, which both contain the TRPA1 agonist allyl isothiocyanate. In snakes, however, the wasabi receptor has taken a very different evolutionary trajectory – it is a highly effective sensor of IR energy and is, in fact, the most temperature-sensitive vertebrate ion channel ever discovered.

The snake TRPA1 channel opens at temperatures of 28°C and above, which is consistent with the sensitivity of the pit organ to thermal changes in the environment (Gracheva *et al.*, 2010). The TRPA1 receptor is thought to mediate thermotransduction in both the modern pit vipers as well as in the ancient boas and pythons, and has therefore evolved convergently in these two snake groups (Gracheva *et al.*, 2010). It was also recently shown that vampire bats use a similar protein, the TRPV1 receptor, to mediate their infrared capabilities (Gracheva *et al.*, 2011). Thus, it seems that the co-opting of somatosensory TRP receptors as heat sensors is a common solution for mediating IR vision, and has evolved convergently in at least three different groups of vertebrates.

1.5.3 Brain processing and cross-modal integration

Thermal vision is inextricably linked to normal vision, and this is reflected in the processing of these two sensory modalities in the snake's brain. In the normal visual system, spatial information from the retina projects, via the optic nerve, to the superficial layers of the contralateral optic tectum in the midbrain, where cells form a topographic map. The rostral-caudal axis of the map represents azimuth in the real world, with the front being straight ahead, and the medial-lateral axis maps elevation, with the medial aspect representing points above the horizon and the lateral aspect points below the horizon.

IR visual information, as part of the somatosensory system, follows a different pathway, but also eventually projects to the optic tectum. The TNMs at the pit organ project ipsilaterally via two ophthalmic branches and one maxillary branch of the trigeminal nerve (Figure 1.11)¹⁹. These first project to an area in the medulla known as the **lateral descending tract of the trigeminal nerve** (LTTD), and then to the **reticulus caloridis** (RC), where it is thought that the signals from the pit organ are refined to improve image quality. Finally, the signals converge onto deep layers in the contralateral optic tectum. Here, the IR information is mapped with the same orientation as the visual information, but at higher magnification. The infrared-sensitive map thus corresponds to only the more central region of the visual map, but other than this expansion, the visual and IR maps of space are roughly in register with one another (Figure 1.11). This suggests that the two separate sensory systems at least partly merge to form a single, coherent representation of the world in the snake's brain (Hartline *et al.*, 1978).

Further evidence for cross-modal integration between visual and IR sensory information comes from recordings of the tectal cells themselves (Newman and Hartline, 1982; Hartline *et al.*, 1978). In addition to unimodal cell types (i.e. purely visual, purely infrared),

¹⁹The innervation pattern of the boid snakes is more complex and varies from species to species.

a large number of **bimodal** tectal cells were found, which were responsive to visual and thermal stimuli in an interactive manner (Figure 1.11)²⁰. Some bimodal neurons, termed *OR* cells, responded to either visual or thermal stimuli, but fired most intensely to input from both modalities presented simultaneously. Other cells, termed *AND* cells, did not respond to either modality alone, but did respond to *simultaneous* visual and infrared stimulus presentation (Hartline *et al.*, 1978).

More complex cell types with non-linear response characteristics were also discovered, such as cells which would fire only to one of the modalities alone, but their activity would be *enhanced* or *depressed* by simultaneous stimuli from the other modality. This led to the identification of six classes of tectal neuron – AND, OR, visual-enhanced infrared, infrared-enhanced visual, visual-depressed infrared and infrared-depressed visual (Newman and Hartline, 1981). From these six classes of neuron, the snake can construct an integrated bimodal visual map of its environment.

The cross-modality of the visual and IR sensory systems coordinates both spatial attention and feature detection mechanisms for prey capture. Firstly, as we saw earlier in the toad, the optic tectum is intimately involved in the control of the spatial direction of attention and orienting movements, and it projects to motor centres in the brainstem and spinal cord involved in coordinating predatory strikes. It is conceivable that the properties of the bimodal tectal cells could give rise to a kind of dual vision, in which both visual and IR cues in the visual field (e.g. information from a warm-blooded rabbit) would excite the snake's attentional processes, orient the snake and initiate a predatory strike (Newman and Hartline, 1981).

If we imagine that a pit viper is hunting in the daytime, and a rabbit hops into the snake's field of view, the OR cells and the 'enhanced' cells would be firing most intensely in the region of the tectum corresponding to the position in space of the warm rabbit, drawing attention to this region. Moreover, the AND cells would be firing *only* in the region of the optic tectum corresponding to the rabbit, as the surrounding cooler regions of the field of view would not provide the thermal stimulation required for the AND cells to fire.

These cell types can be considered to be innovative feature detectors (see earlier in this chapter), where the normal features of the visual system (shape, orientation, motion direction) are supplemented by features from an extra sensory modality. For instance, the AND cells could be considered **prey detectors**, or **mouse detectors** (Newman and Hartline, 1982), analogous to the worm-detector cells we discussed earlier in the toad visual system, where specific shape, size and motion information, as well as information about thermal profile, all combine to signify prey. The combined processing of features from two overlapping sensory modalities would increase the sensitivity of the snake's prey detection system, which may otherwise remain silent under certain conditions, such as during the dark of night.

1.5.4 Behaviour

The neurobiology of thermal vision is fascinating, but what is the evidence that these snakes actually use this unique sensory system for predator-prey interactions? After all, there are more snake species without pit organs than there are with them (De Cock Buning, 1983). The predatory strike of the rattlesnake consists of a rapid bite phase in which venom is injected, followed by a quick release of the prey, and then the snake

²⁰The integration of different sensory modalities at the optic tectum occurs in many animals; for example, there is integration of visual and electrosensory information in electric fish.

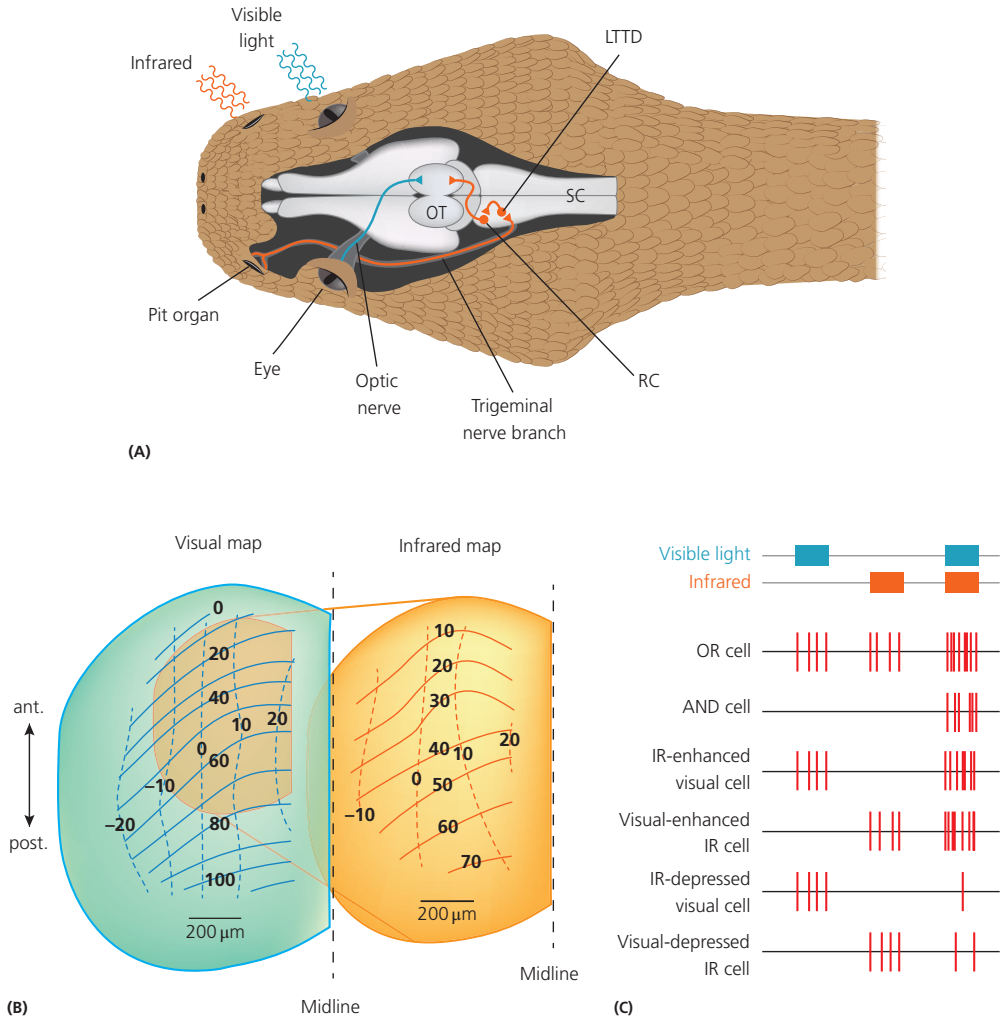


Figure 1.11 Processing of visual and infrared information in the snake brain. **A:** Schematic of the head of a pit viper, showing the neural pathways for processing visible light (blue) and infrared radiation (orange). For normal vision, light is transduced via a photochemical process in the retina of the eye and signals are sent via ganglion cells through the optic nerve to the optic tectum. For infrared processing, infrared light is transduced at the pit organ membrane through the activation of TRPA1 channels present in TNMs. Signals are sent via the trigeminal nerve branch to the LTLD and RC for processing, before converging with visual information in the optic tectum. SC = spinal cord; OT = optic tectum; LTLD = lateral descending tract of the trigeminal nerve; RC = reticulis calor. **B:** Top-down view of the visual and infrared topographic maps in the left optic tectum. The infrared map, which lies below the visual map but in the diagram is offset to the right for clarity, represents a magnified region of the central space in the visual map. In the anterior-posterior direction, the numbers indicate the azimuth bearing, with 0° being straight ahead. In the medial-lateral direction, the numbers indicate elevation, with positive values being above the horizon. Data from Hartline *et al.* (1978). **C:** Response properties of the six identified neuron classes in the optic tectum to visible and infrared light stimuli. Adapted from Newman and Hartline (1982).

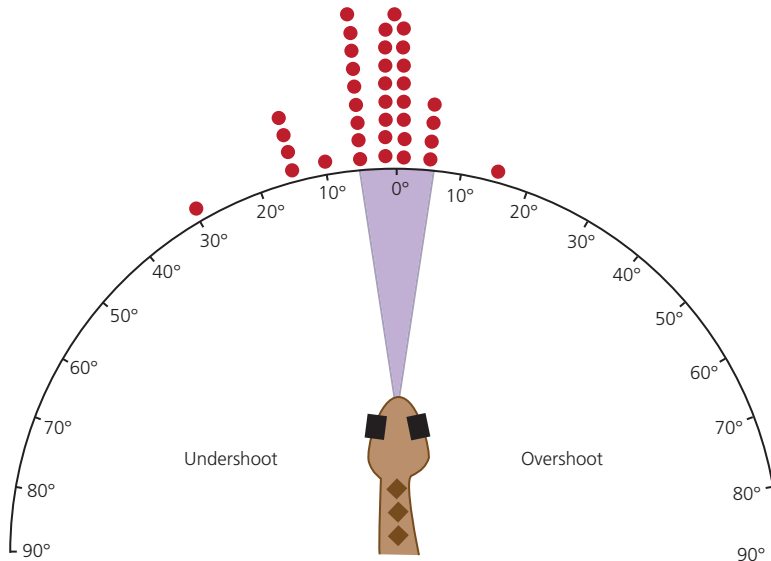


Figure 1.12 Infrared vision is sufficient for accurate predatory strikes. The accuracy of thermal vision in snakes was demonstrated by presenting a warm object at varying degrees to the left or right of a snake whose eyes have been covered using blinders. Each red circle represents a strike by the snake and is located at the angular error between strike and target. The purple shaded area illustrates the average error, which was around $\pm 5^\circ$. Adapted from Newman and Hartline (1982).

withdraws, so as to avoid retaliation from the prey. The whole sequence is over in less than half a second, so there is an acute need for accuracy. A misplaced bite may result in less effective envenomation, while simultaneously alerting the prey to the snake's presence and, if the strike is particularly off-target, the snake risks impaling itself on a prey animal's tooth or claw (Kardong and Smith, 2002).

Infrared-sensitive snakes that have been artificially blinded (or are congenitally blind) in the normal visual spectrum are still able to strike a target with only slightly reduced accuracy compared to snakes with full visual capability (Figure 1.12; Newman and Hartline, 1982; Kardong and Mackessy, 1991; Chen *et al.*, 2012). This shows that infrared vision alone provides sufficient information for accurate coordination of predatory strikes. Moreover, such blind snakes still successfully strike the more vulnerable regions of prey (such as the back of the head), suggesting that thermal vision is of sufficient detail that it can compensate for loss of normal vision and maintain accurate targeting of prey. However, when the pit organs are blocked, normal vision alone is also sufficient for predatory strikes in daylight, with only slightly reduced accuracy compared to intact animals, demonstrating that thermal vision is not *required* for accurate strikes, but does assist in accuracy.

When both the eyes and the pit organs are occluded, the snakes are unable to initiate a predatory strike at all (Kardong and Mackessy, 1991; Haverly and Kardong, 1996; Chen *et al.*, 2012). Thus, normal and thermal vision are the primary senses involved in coordinating predatory strikes in these snakes, with each sense sufficient by itself for highly successful prey capture. Infrared-sensitive snakes are ambush predators that often hunt at night or in dark burrows, which gives them a huge sensory advantage, since their thermal vision is apparently sufficient to compensate for the loss of normal vision – a luxury the prey will not have.

In addition to detecting warm-blooded prey, pit organs are also used to identify cool spots in the environment to which the snake can retreat in the heat of the day for behavioural thermoregulation. Indeed, it has been suggested that this may have been the original function of pit organs, which only later became later redeployed for prey capture (Krochmal *et al.*, 2004; Bakken and Krochmal, 2007).

1.5.5 Infrared defence signals

Snakes and squirrels have battled for millennia in an ancient predator-prey relationship that has led to fascinating specialisations in both animals. For example, rattlesnakes (*Crotalus* sp.) possess a powerful cocktail of deadly venom, but the Californian ground squirrel (*Otospermophilus beecheyi*) has evolved apparent immunity to these toxins (Rundus *et al.*, 2007). Similarly, while rattlesnakes have evolved infrared vision as a sensory supplement used for prey capture, recent evidence demonstrates that ground squirrels actually exploit this infrared ability in their defence behaviour (Rundus *et al.*, 2007; Barbour and Clark, 2012).

When a Californian ground squirrel detects an encroaching rattlesnake, it will often stand its ground rather than escape, especially if there is a burrow nearby containing pups (which *are* vulnerable to snake toxins until they reach one month old). The squirrel might flick sand or dirt towards the predator, or even deliberately attack it. It also sends out a strong visual signal – **tail-flagging** – whereby its tail is strongly erected and wagged back and forth in plain sight of the snake. It may seem unwise for the squirrel to deliberately advertise itself and aggravate a predator but, since it is immune to the snake's main weapon, venom, then without a well-placed strike the squirrel has a high chance of coming out of a tussle injured but alive (a lose-lose outcome for both parties). The squirrel is therefore sending a **predator deterrent signal** to communicate that it is aware of the snake's presence and is not going to be an easy target. The predatory snake will usually respond to tail-flagging by switching from an aggressive stance to a defensive one, and will slither off with its tail metaphorically between its legs.

Rundus *et al.* (2007) have discovered a remarkable hidden complexity to the tail-flagging behaviour. When viewed through an infrared camera, the squirrel's tail glowed a bright red during tail-flagging when it encountered a rattlesnake (Figure 1.13²¹). It transpires that these squirrels deliberately flood their tails with blood, to generate an additional infrared component to their predator deterrent signal. This behaviour is not a general response to predation – the squirrels *only* heat their tails during encounters with infrared-sensitive snakes (such as rattlesnakes, *Crotalus oreganus*), but not during encounters with *non*-infrared-sensitive snakes (such as gopher snakes, *Pituophis melanoleucus*). It seems, therefore, that squirrels are not only using motion in their tails as a visual predator deterrent (and conspecific alarm) signal, but they are also conveniently translating the signal into a second sensory modality for the infrared-sensing snakes. This is remarkable – not least because the squirrels themselves are essentially blind to the very sensory system they are using to communicate.

The function of the infrared signal in the wild has been tested using a stuffed robotic squirrel imaginatively named 'Robosquirrel' (Figure 1.13 C,D; Rundus *et al.*, 2007), which has a tail whose movement and temperature can be remotely controlled. As expected, simple tail-flagging by the robotic squirrel caused predatory snakes to switch from attacking to defensive behaviour, and reduced the number of predatory strikes, compared with

²¹See www.pnas.org/content/suppl/2007/08/09/0702599104.DC1 for videos.

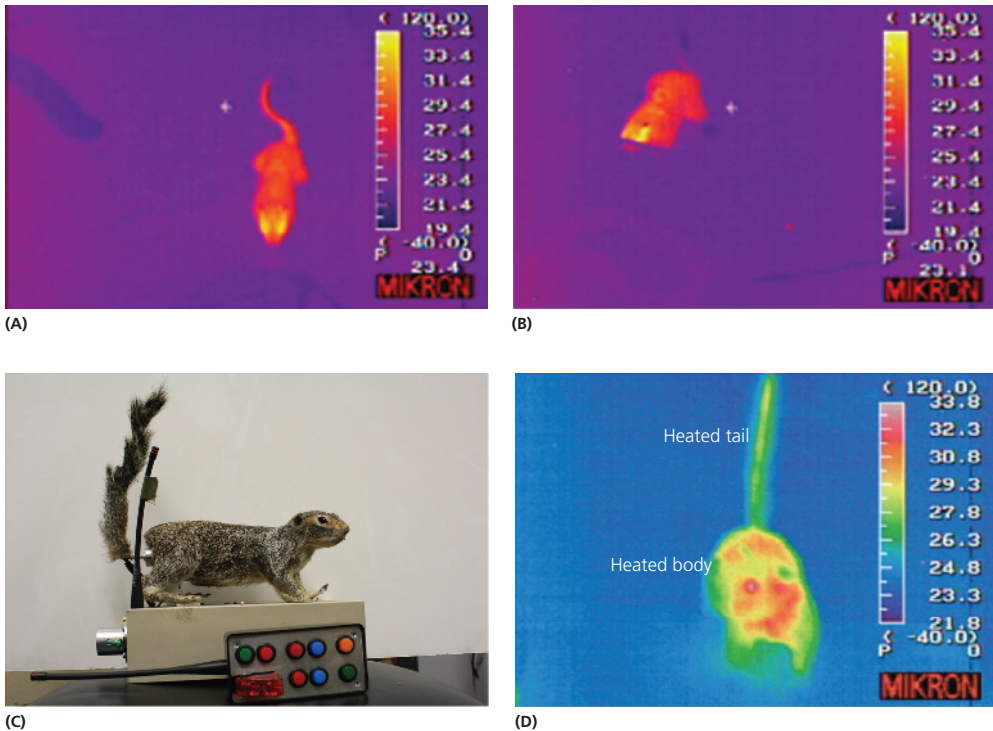


Figure 1.13 Infrared predator deterrent signals. **A:** An encounter between a Californian ground squirrel and a rattlesnake, viewed using an infrared camera. The squirrel floods its tail with blood to generate infrared radiation for its tail-flagging behaviour. **B:** An encounter between a squirrel and a non-infrared-sensing species of snake. Note the absence of the infrared component at the tail. A, B from Rundus *et al.* (2007), with permission from National Academy of Sciences, USA. **C, D:** Rundus *et al.* (2007) constructed a robotic squirrel whose tail movement and temperature could be remotely controlled, allowing the researchers to study the function of the infrared component during encounters with snakes in the wild. See text for details. C courtesy of Sanjay Joshi, University of California, Davis, D adapted from Joshi *et al.* (2011), with permission from Aaron Rundus.

no tail-flagging. However, this effect was significantly more pronounced with the inclusion of the infrared tail component, demonstrating the importance of the infrared component of the signal in its natural context. Thus, squirrels deliberately heat their tails to create an infrared signal to advertise their vigilance to thermal-sensitive snakes, which subsequently causes the latter to back down from what might otherwise be a less-than-effective predatory strike (Rundus *et al.*, 2007; Barbour and Clark, 2012). The infrared component presumably becomes even more important during conditions of low light, when the non-infrared components would no longer be visible to the snake. Indeed, these squirrels are known to tail-flag more frequently during encounters in the dark (Coss and Owings, 1978; Rundus *et al.*, 2007).

The defensive signals used by squirrels have been sculpted by evolution to the animals they encounter. For avian or mammalian predators, squirrels favour vocalisations for defensive communication (Rundus *et al.*, 2007). During encounters with snakes, which are largely insensitive to airborne acoustic signals, squirrels instead favour visual communication. These visual signals are tailored even further to the individual snake species – snakes that have evolved multi-modal visual senses (normal and infrared) have enabled the co-evolution in squirrels of multi-modal visual defence signals.

1.6 Aerial predators: dragonfly vision

Visual processing in sit-and-wait predators such as toads and snakes is complex enough, but aerial predators perform similar functions while simultaneously coordinating complex flight patterns. The associated visual demands of capturing a moving object in mid-air are highly complicated, as not only do these animals need to detect relevant features of their prey, but features which are constantly moving along the x -, y - and z -axes, owing to simultaneous self and prey motion. They also have to distinguish their prey from a complex and constantly shifting background during the pursuit. Moreover, aerial insects do so using a relatively small nervous system, compared with the previously described vertebrates.

Despite these obstacles, one aerial predator – the **dragonfly** – is a spectacularly adept hunter which can capture other flying insects mid-air with a success rate of over 95% (Gonzalez-Bellido *et al.*, 2013)²². Dragonflies are ancient animals with fossil records dating back 300 million years. While their overall body size has changed dramatically since then (they once had hawk-sized bodies, with a wingspan of nearly a metre), the wing structure and flight mechanism of modern dragonflies is thought to be roughly the same as that of the dragonflies that preceded the dinosaurs (Hurrell, 2012). In this final section of the vision chapter, we will look at how dragonflies capture their prey during aerial pursuits and use their visual system to correct for sudden changes in prey movement, to ensure successful capture at almost every single attempt.

1.6.1 Dragonfly eyes

Dragonflies possess compound eyes that are huge relative to their body; they literally wrap around most of the surface of the animal's head, providing almost 360° vision, which not only helps to pursue prey in front of the animal, but also to detect predators approaching from behind (Figure 1.14)²³. The massive size of their eyes is partly due to the fact they



Figure 1.14 Dragonfly eyes. Dragonflies possess the most complex eyes of all insects and have around 300 000 individual ommatidia. Photographs courtesy of Keith Sillar.

²²This is an exceptionally high success rate; apex predators such as lions, tigers and sharks only capture their prey around 25–50% of the time.

²³Unlike many insects, dragonflies do not have a visual blind spot, which is part of the reason they are so notoriously hard to catch!

have a huge number of individual facets, with up to 30 000 ommatidia per eye. The structure and function of each eye is not uniform, but instead contains a specialized region called the **dorsal acute zone**. This narrow crescent-shaped zone of high resolution is located about 55° above the horizon and contains ommatidial facets much larger than elsewhere in the eye, and with much more closely aligned optical axes. Overall, this produces a narrow upward- and forward-facing fovea, about 20° in height and around 60° above the horizon (Olberg *et al.*, 2007). This region is also highly sensitive to short wavelength (blue and UV) light, which is useful when chasing small flying objects that appear black against the UV-radiating backdrop of a blue sky (Olberg, 2012). During aerial pursuit, the dragonfly rotates its head to keep the target prey stabilised in the ‘crosshairs’ of this dorsal acute zone (Olberg *et al.*, 2007; Gonzalez-Bellido *et al.*, 2013).

1.6.2 Aerial pursuit

The navigational problem for the dragonfly, as for any pursuit predator, is to ensure that it and its prey arrive at the same point in space at the same time. Some predators use a surprisingly simple solution. In order to ensure interception with a prey animal, all the predator has to do is steer itself so as to maintain its target at a fixed angle relative to its own direction of travel. Then, as long as this angle is less than 90° from straight ahead, and as long as the pursuer is faster than its target, predator and prey will always eventually collide (Olberg *et al.*, 2000). This is an example of a **constant bearing, decreasing range** (CBDR) situation, and these have long been used by mariners as predictors for the likely collision of ships at sea. A pursuit strategy such as this is useful, as it does not require the pursuer to have any information about the size, distance or velocity of the pursued; it simply needs to correct for any changes in the direct line-of-sight angle²⁴.

Keeping a constant bearing (with decreasing range) will ensure eventual collision, but what is the *best* bearing to keep constant? Predators (and also animals chasing after potential mates) utilise various different strategies (Figure 1.15). Many insects use simple **tracking** (or **classical pursuit**), in which the pursuer always aims directly at the target (a constant bearing of zero); so long as it can move faster than the target, it will obviously eventually catch it up. However, this is not very efficient, and often results in long, spiral chases (Olberg *et al.*, 2000).

A more economical strategy is **interception**. Here, the pursuer aims for a point in *front* of the target, thus taking account of the distance the target will have moved in the time it takes to catch up with it. This is essentially equivalent to deflection shooting. If the target maintains a steady course, then the optimal bearing to ‘cut the corner’ only has to be calculated once and, thereafter, the predator can maintain CBDR while flying in a straight line. However, if the target makes evasive manoeuvres, then the optimal bearing will need updating.

Various raptors have been shown to use this interception strategy for prey capture, including barn owls (Fux and Eilam, 2009), falcons (Kane and Zamani, 2014) and goshawks (Kane *et al.*, 2015). Interestingly, it has also been suggested that some of the evasion tactics displayed by raptor prey are effective because they thwart the CBDR strategy. For example, voles and pheasants often make abrupt and sharp sideways movements when being pursued by a raptor, which would presumably lead to a loss of visual fixation in the predator that is too large and sudden to be corrected for (Kane *et al.*, 2015).

²⁴An optimal strategy to achieve a fixed bearing approach with a moving target is a guidance law known as **proportional navigation**, in which the pursuing object always changes course at a rate proportional to the rate of change in the direct line-of-sight angle with the target. This is a guidance law used by most homing missile systems designed to intercept airborne targets.

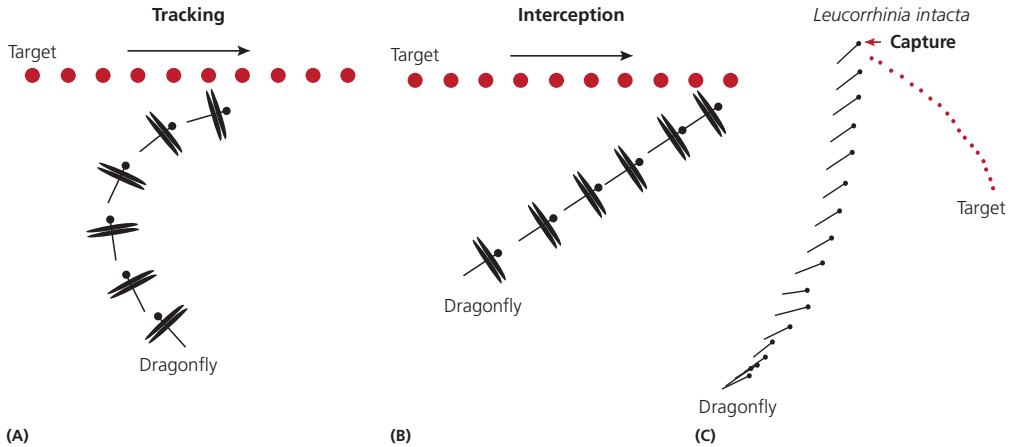


Figure 1.15 Prey pursuit strategies. **A:** A diagram showing a top-down view of the tracking strategy. The chaser aims directly at the target, steering its movement to maintain the target straight ahead at all times. **B:** A diagram showing a top-down view of the more economical interception strategy. The chaser aims ahead of the target and intercepts it by aiming for the anticipated future collision point. **C:** Experimental data showing frame-by-frame analysis of a side-on view of a dragonfly (*Leucorrhinia intacta*; line indicating body, dot indicating head) pursuing its prey (red dot). The prey is rising through the air, and the dragonfly attacks from below on an interception course. Note that the prey is maintained within the dorsal acute zone fovea throughout the pursuit. A, B adapted from Collet and Land (1978), C adapted with permission from Olberg *et al.* (2000).

In terms of neural processing, the simplest method for achieving prey interception is to use a **reactive strategy**, in which deviations in prey visual angle are detected by specific neurons in the visual system and responded to with compensatory movements, much like an autopilot mechanism. An alternative, but far more complex, way to achieve interception is to use a **predictive strategy**, whereby movements are pre-planned, based on internal models of self and prey motion. Predictive strategies involve complex neural processing, and were traditionally thought only to be used by vertebrates for complex sensorimotor tasks. However, recent evidence suggests that dragonflies use a combination of both reactive *and* predictive neural computations to achieve interception of their prey (Mischiati *et al.*, 2014).

1.6.3 Predictive foveation

Dragonflies possess four wings, which can be controlled independently, allowing for complex flight movements, including hovering, sideways rolls, flying up, down, left and right, and even upside-down. During prey pursuit, they use this agility to ensure optimal body orientation. They use wing movements to make regular rotations, so as to align their body and bearing with the prey's direction of movement, and then approach from below, where detection by the prey is least likely to occur (Mischiati *et al.*, 2014). During the approach, they swoop up and close the vertical distance, and then use their outstretched front legs to cut off the prey's escape route and scoop the insect into their mouth, to be engulfed mid-air (Olberg *et al.*, 2000)²⁵.

²⁵Some species of dragonfly are sit-and-wait aerial predators, which perch on branches or vegetation until a flying insect passes by, at which time the dragonfly engages in aerial pursuit. Other species of dragonfly stay in flight continuously ('hawkers'), and swoop upwards to pursue prey that passes above them (Olberg, 2012).

Prey motion, as well as self-motion due to body rotations, introduces significant prey image drift on the retina, so how do dragonflies keep the target fixed on its fovea? High-speed video recordings show that the dragonfly performs compensatory head movements, independent of body movements, so as to cancel out the image drift and keep the prey perfectly fixed within the dorsal acute zone of the retina. These head movements have been shown to occur in near synchrony with the retinal image drift, with a near zero lag (≈ 4 ms). They therefore cannot be explained by sensory feedback error correction, and suggest that the dragonfly generates internal models of its own body dynamics and the expected target motion (Mischiati *et al.*, 2014). Thus, for prey moving on a fixed trajectory, a dragonfly carries out sophisticated computations to determine exactly what head movements are required to compensate for both its own body movements and those of the target, and to ensure that the target remains fixed in its retinal fovea during the path to interception. As yet, the neural circuitry underpinning this **predictive foveation** remains to be elucidated.

1.6.4 Reactive steering: STMDs and TSDNs

Predictive models allow the dragonfly to pursue its prey with remarkable speed and accuracy, using perfectly-timed head adjustment to compensate for retinal drift and keep the target prey fixated in the dorsal acute zone. But what happens if the target prey produces a sudden unexpected change in its trajectory? The dragonfly cannot predict and pre-plan for such prey movement, and specific sets of neurons in the dragonfly visual system appear to be involved in detecting these sudden changes and initiating compensatory head and wing movements.

Like vertebrates, insects have feature detectors in their visual pathway – that is, neurons which extract elements of a visual stimulus by responding only to highly specific features, and whose activity is important in initiating or coordinating a specific behaviour. The first such neurons found in the dragonfly occur in the third optic neuropil – the **lobula complex**. This contains **small target motion detector** (STMD) neurons that are exquisitely and preferentially sensitive to the movements of small objects in a broad range of directions, but which are insensitive to movements of the visual field as a whole (Olberg, 2012). The preferred size range (subtending $1\text{--}2^\circ$) is precisely that occupied by targets such as fruit flies or mosquitoes, at the range at which dragonflies most readily initiate pursuit (Combes *et al.*, 2013). The STMDs, in turn, drive eight pairs of descending interneurons, called **target-selective descending neurons** (TSDNs), which transmit target motion information to the thoracic motor centres and result in adjustments to wing movement (Gonzalez-Bellido *et al.*, 2013).

There are several properties of the TSDN neurons which suggest that they act as feature detectors that specifically detect sudden changes in prey motion, and initiate compensatory wing movements during aerial pursuit. They have specific dorso-frontal receptive fields which extend to the critical dorsal acute zone; these remain completely silent unless presented with a target of the preferred size in the cell's receptive field moving in a highly specific direction, and the strength of their response is proportional to the angular speed of the visual stimulus. Experimental stimulation of these TSDNs results in changes in wing position/angle, which have been interpreted as steering movements.

Finally, the TSDNs are large neurons, with the fastest conducting axons in the dragonfly nervous system. This is important, as compensatory wing movements occur with a latency as short as 26 ms (Frye and Olberg, 1995; Olberg *et al.*, 2007; Olberg, 2012). Recent research has provided further evidence that the TSDN neurons perform a role in

commanding flight during aerial prey pursuit. Gonzalez-Bellido *et al.* (2013) found that the 16 TSDNs act collectively as a **population vector**²⁶. The individual TSDNs have overlapping receptive fields and direction tuning curves, and also have similar response latencies. The net activity of these partly overlapping TSDN neurons encodes the direction of prey movement.

The TSDNs can be considered ‘error-detectors’, responsible for detecting and compensating for unexpected retinal slip. During aerial pursuit, the dragonfly rotates its head using predictive foveation, so that the prey item is stabilised in a fixed position in the high-acuity dorsal acute zone of its retina which, for prey moving along a fixed trajectory, appears to be sufficient for prey capture. However, if the prey suddenly changes direction during the pursuit, the position of the prey on the retina will move at a particular speed and direction away from the ‘sweet spot’ on the retina, which is detected by TSDN neurons tuned to movements in this direction and velocity. The net activity of the TSDN population encodes an error between the desired approach bearing and real-time bearing, which is then countered by compensatory steering movements mediated by changes in wing angle and position. This mechanism, whereby retinal slip is minimised through corrective head and wing adjustments, ensures the likely eventual collision between predator and prey, even if the prey makes sudden unexpected changes in its trajectory.

1.7 Summary

One of the most important tasks for an animal is to distinguish between a predator (bad news) and food (good news), and the visual system of many animals involves a reliable feature-recognition system for performing this function. Toads distinguish between prey-like and predator-like visual stimuli using parallel processing streams, which converge onto feature detector cells (T5.2 cells) in the optic tectum. The activity of these cells ultimately dictates whether the animal responds with an attack sequence of behaviour towards an object in space.

One of the most fascinating and unique visual systems is that of crotalid and boid snakes, which transduce light outside the visible spectrum to hunt in complete darkness. These snakes possess pit organs containing a thermal-sensitive membrane expressing a novel receptor, typically associated with pain sensation, which has been repurposed as an infrared sensor to convert infrared radiation into neural activity. This information passes, again, to the optic tectum, where it becomes integrated with the canonical visual system to provide supplementary feature information that facilitates the detection, recognition and capture of prey.

There are exceptionally heavy visual demands placed on a flying predator, yet the ancient dragonflies have evolved highly successful solutions to these problems. Dragonflies use their agility to align their bodies in the most efficient and appropriate orientation as they hurtle towards a prey interception point, while approaching the prey from below so as to avoid detection. Using a combination of predictive and reactive strategies, they perform head rotations to compensate for prey image drift, and ensure that the pursued target remains tightly fixed in the crosshairs of the retina, the dorsal acute zone. The

²⁶A population vector refers to the sum of preferred directions of a group of neurons with different directional selectivity.

neural circuitry underlying the predictive model remains to be elucidated, but the activity of a small set of TSDN neurons in the visual system appear to be responsible for reacting to sudden changes in prey trajectory. The combination of predictive and reactive strategies ensures successful interception and prey capture with almost every single attempt, and all this is achieved using a much smaller nervous system than that of vertebrates performing similar computations. This makes dragonflies one of the most successful aerial predators in the animal kingdom.

Abbreviations

CBDR	constant bearing, decreasing range
EM	electromagnetic
IR	infrared
LTTD	lateral descending tract of the trigeminal nerve
NO	nitric oxide
RC	reticulis caloris
STMD	small target motion detector
TNM	terminal nerve mass
TRPA1	transient receptor potential Ankyrin 1
TSDN	target-selective descending neuron
UV	ultraviolet

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