Citation: Douglas, R. H. (2018). The pupillary light responses of animals; a review of their distribution, dynamics, mechanisms and functions.. Progress in Retinal and Eye Research, 66, pp. 17-48. doi: 10.1016/j.preteyeres.2018.04.005

This is the accepted version of the paper.

This version of the publication may differ from the final published version. To cite this item please consult the publisher's version.

Permanent repository link: https://openaccess.city.ac.uk/id/eprint/19785/

Link to published version: https://doi.org/10.1016/j.preteyeres.2018.04.005

https://doi.org/10.1016/j.preteyeres.2018.04.005

The pupillary light responses of animals; a review of their distribution, dynamics, mechanisms and functions

Ronald H. Douglas

Division of Optometry & Visual Science
City, University of London
Northampton Square
London EC1V 0HB
U.K.

r.h.douglas@city.ac.uk

Abstract

The timecourse and extent of changes in pupil area in response to light are reviewed in all classes of vertebrate and cephalopods. Although the speed and extent of these responses vary, most species, except the majority of teleost fish, show extensive changes in pupil area related to light exposure. The neuromuscular pathways underlying light-evoked pupil constriction are described and found to be relatively conserved, although the precise autonomic mechanisms differ somewhat between species. In mammals, illumination of only one eye is known to cause constriction in the unilluminated pupil. Such consensual responses occur widely in other animals too, and their function and relation to decussation of the visual pathway is considered. Intrinsic photosensitivity of the iris muscles has long been known in amphibia, but is in fact widespread in other animals. The functions of changes in pupil area are considered. In the majority of species, changes in pupil area serve to balance the conflicting demands of high spatial acuity and increased sensitivity in different light levels. In the few teleosts in which pupil movements occur they do not serve a visual function but play a role in camouflaging the eye of bottom-dwelling species. The occurrence and functions of the light-independent changes in pupil size displayed by many animals are also considered. Finally, the significance of the variations in pupil shape, ranging from circular to various orientations of slits, ovals, and other shapes, is discussed.

Keywords; pupil, iris, constriction, dilation, vertebrate, cephalopod

Abbreviations

PLR	Pupil Light Response
OPN	Olivary Pretectal Nucleus
EWN	Edinger-Westphal Nucleus
ipRGC	intrinsically photosensitive Retinal Ganglion Cell
CG	Ciliary Ganglion
t_{50}	Time after light exposure at which 50% constriction is reached

Contents

1. Introduction

In this review, the term pupil is restricted to the aperture formed by the iris in the simple eyes of vertebrates and cephalopods. In most of these animals, the size of the pupil changes depending on the ambient illumination, increasing in area as light levels fall. Invertebrate compound eyes also have what is termed a ‘pupil’ formed by migration of screening pigment between the rhabdoms, altering photoreceptor illumination (Warrant & McIntyre, 1996; Land & Nilsson, 2012). Such pigment migrations are not considered here.

The functions of, and the mechanisms behind, the variations in human pupil diameter are well known. The reasons for the extensive literature covering the human pupil are manifold: Those interested in the biology and optics of vision study the pupil as it is an important mechanism that helps balance the conflicting demands of optimising sensitivity and spatial acuity in different light conditions and for different visual tasks. However, the size of the pupil is not only related to vision and ambient illumination, and can be influenced by, for example, cognitive load and arousing stimuli. The pupil is therefore also of interest to those investigating various psychological phenomena. Understanding the neural and muscular mechanisms underlying changes in pupillary area is also important to clinicians, as they need to alter the area of the pupil pharmacologically during eye examinations. Perhaps most importantly, however, abnormal pupil responses are a powerful indicator of central nervous system pathology and trauma indicating, for example, the presence and location of tumours, cardiovascular anomalies, neurodegenerative disease, and other lesions. For all these reasons, the human pupil has been thoroughly researched and extensively reviewed.

However, much less is known about the pupil responses of other animals and no comprehensive reviews are available. Although Walls's seminal book on comparative vision (Walls, 1942) includes references to the pupil, it is not the focus of the work. Similarly, Loewenfeld's classic book on the pupil (Loewenfeld, 1993) concentrates on the human pupil, although it does contain references to historical work on other animals. This review will attempt to fill this gap and compare the pupil responses of other vertebrates and cephalopods to those of humans.

There are approximately 65,000 extant species of vertebrate (The World Conservation Union, 2014), divided here into fish, birds, reptiles, amphibia and mammals, as well as 600-800 living species of cephalopod (Nesis, 1987; Hanlon & Messenger, 1996). The pupil responses of only a tiny fraction of these have been examined. It is also unreasonable to expect, for example, the pupils of all 25,000 species of fish to behave in exactly the same way. One therefore cannot talk about the pupil response of 'the fish', or any other group of animals. This review therefore cannot hope to be comprehensive. Instead, it will attempt to give an overview of the pupil response within different groups of animals using representative examples.

2. Iris structure

Although the detailed structure of the iris varies between species, all have basic similarities. The iris of humans will serve as a representative example.

The iris is the most anterior part of the uvea, which at its base is attached to the ciliary body from which it extends inwards (Fig. 1A) forming a circular aperture, the pupil. It separates the anterior and posterior chambers of the eye and is bathed in aqueous humour. Unusually for an exposed surface, the anterior iris is not covered by an epithelium; instead consisting of a dense network of interwoven fibroblasts posterior to which is a layer of melanocytes, whose thickness influences the colour of the iris. The iris stroma is an example of an aereolar connective tissue made up of loosely arranged collagen fibres containing a variety of cell types (e.g. fibroblasts, phagocytes, melanocytes, mast cells), nerves, and blood vessels. The insubstantial nature of the stroma allows the iris to change shape during muscular contraction, thereby regulating pupil size. Posteriorly, the iris is covered by a double-layer of pigmented epithelial cells (Fig. 1), whose cells are connected by numerous junctions to ensure they do not separate during iris movement (Bron et al., 1997).

The irises of other animals differ in detail from that outlined above for humans. For example, the iris stroma in many animals, such as frogs (Nolte & Pointner, 1975), toads (Rubin et al., 1986), fish (Kuchnow & Martin, 1970; Lanzing & Wright, 1981; Munk, 1985), and octopus (Froesch, 1973), contains layers of melanophores, iridophores and xanthophores. Furthermore, the front surface of the octopus (Froesch, 1973) and fish (Lanzing & Wright, 1981; Munk, 1985) irises are formed by an epithelium, rather than the insubstantial anterior border layer described above for humans. However, something the irises of all normally pigmented animals have in common is that their posterior surfaces are covered by epithelia containing dense melanin, allowing the iris to function as an efficient aperture stop.

Another thing most irises share is the presence of muscle. The majority of species have a narrow circular sphincter pupillae running circumferentially around the pupillary margin (Figs. 1A&B & 2A&C), whose contraction decreases pupil diameter. Many species also have a radial dilator muscle between the sphincter muscle and the iris root that increases pupillary area on contraction (Figs. 1A&C, 2). In animals with slit-like pupils, the sphincter muscle is not circular and instead is divided into several bundles two of which cross and run vertically (Raselli 1923; Section 9.2.1; Fig. 2B). While the sphincter muscle usually lies within the iris stroma and is separated from the pigmented epithelium (Fig. 1B), the dilator is normally myoepithelial and is located within the cells of the posterior epithelium (Fig. 1C).

The degree to which these two muscles are developed varies between species. While a sphincter muscle has been reported in most animals examined, the dilator is often absent. In animals where the iris is directly involved in accommodation, such as amphibious species (Section 8.3.2), the iris muscles, especially the sphincter, are particularly well developed (Ballard et al., 1989).

Classically, the iris muscles are described as unstriated in mammals, fish, and amphibia, but striated in birds and reptiles. However, both pharmacological and histological work suggests the irises of some reptiles (Iske, 1929; Reger, 1966) and many birds in fact contain both striated and non-striated muscle components (Gabella & Clarke, 1983; Yamashita & Sohal, 1986; Scapolo et al., 1988; Barrio-Asensio et al., 1999; Loerzel et al., 2002). Although the non-striated tissue can be located throughout the iris in smooth muscle cells within the stroma, it often forms a distinct myoepithelial dilator muscle (Walls 1942 for review of earlier literature; van Oehme, 1969; Nishida & Sears, 1970; Oliphant et al., 1983; Dieterich et al., 1988). In chicks, unstriated iris muscle is particularly apparent early in development, after which there is a transition to striated fibres, although some unstriated muscle is retained even in adults (Pilar et al., 1987; Volpe et al., 1993; Link & Nishi, 1998).

Although iris muscles are responsible for changes in pupil size, their simple presence cannot be taken as proof of pupil mobility. The bilby, an Australian marsupial, for example, has an iris sphincter muscle, yet its pupil is immobile (Arrese, 2002; Section 3.1.2.2). Similarly, most teleost fish have pupils that lack significant mobility (Section 3.5.2.3), but many still possess iris muscles (Grynfeltt, 1910; Staflova, 1969) which appear to be innervated (Munk, 1985). We have also shown pronounced circular, and lesser radial, staining for filamentous actin in the irises of the zebrafish, as well as other teleosts, that is consistent with both iris sphincter and dilator muscles (Fig. 3), although these species lack mobile pupils.

It seems reasonable to assume that the function of iris muscles in animals with immobile pupils is to maintain the size and shape of the pupil. In fish, for example, the lens protrudes through the pupil and accommodation occurs via changes in lens position (Sivak, 1980; Ott, 2006). If the iris were lax and not held under tension by some means, such as muscle, the form of the pupil could be affected during accommodation either directly by contact between the lens and the iris or by any resulting changes in aqueous flow (Munk, 1985).

3. Pupil shape and the dynamics of the pupil light response

Although some species have fixed pupils, in most, except at the extremes of illumination, pupil area decreases as light levels rise. The timecourse and extent of this Pupil Light Response (PLR) in different animal groups are reviewed below.

However, detailed comparisons between species must be treated with caution as the dynamics of the PLR will be influenced by a number of factors including; the intensity and spectral composition of the stimulating and background lights, the length of any preceding dark adaptation, and probably additional variables such as the time of day (Section 8.1) and temperature. These are rarely the same in different studies. The use of anaesthetics will also influence the response of the pupil, and where possible we have referred to studies involving unaesthetised animals that were either freely moving or lightly restrained.

Comparison between studies is further complicated by the fact that the size of the pupil is expressed variably in terms of either its diameter or area. Furthermore, these are given either in absolute units or as a proportion of the dark adapted pupil size. Similarly, the time taken for constriction is usually given in terms of how long it takes to complete. However, as this is usually asymptotic it is often difficult to determine accurately. A more precise measure of the speed of constriction is given by the time taken to reach half the fully dilated area (t_{50}), which will be used in this review where possible.

The PLR of humans and other animals is usually studied in the laboratory using brief flashes of, often high intensity, light. However, such stimulation will rarely, if ever, occur in the wild, where changes in illumination, most notably dawn and dusk, are more gradual and prolonged. Although the response of the pupil to gradual changes in illumination is usually not investigated, this review will concentrate on pupillary responses to prolonged changes in illumination where possible.

Pupillary constriction can be evoked by both light falling on the retina and, in many species, by direct illumination of the iris muscles without involvement of the retina. Pupil responses that are independent of retinal illumination will be discussed elsewhere (Section 6). The current section will describe the pupil responses of intact animals, which are the result of both iris and retinal illumination.

3.1 Mammalian pupil responses

The detailed phylogeny of the approximately 5,500 extant mammalian species remains a matter of debate (Meredith et al., 2011). There are 2 broad groupings; the egg-laying monotremes (4 species of echidnas & 1 platypus), and the live-bearing theria. The latter are further subdivided into marsupials (ca. 350 species) and placentals.

3.1.1 Pupil shape

The pupils of many mammals, such as most primates and rodents, remain circular at all light levels, but horizontal or vertical ovals/slits when pupils are constricted are also widespread (Mann, 1931; Walls, 1942; Malmström & Kröger, 2006). Vertical pupils are often associated with carnivores, such as the domestic cat (Fig. 4A&B) and seals, while horizontal pupils are more often found in herbivores, such as kangaroos and many ungulates (Fig. 4D&E). However, Mann (1931) argues that rather than diet, pupil shape is determined mainly by activity cycles, vertical pupils being characteristic of nocturnal animals and horizontally elongated and circular pupils more common in diurnal species. This is discussed further in section 9.2.

In some animals, the iris forms a dorsal operculum or umbraculum within the pupil on constriction (Section 9.1). Among mammals, such protrusions are rare and only observed in the rock hyrax (Millar, 1973) and in some cetaceans (Walls, 1942; Herman et al., 1975; Dawson et al., 1979; West et al., 1991; Kröger & Kirschfeld, 1993; Mass, 2001; Bjerager et al., 2003; Mass & Supin, 2007; Rivamonte, 2009; Miller et al., 2010, 2013), in whom they can form a U- or crescent-shaped constricted pupil, which may form two small apertures at the highest light levels (Fig. 4C). The corpora nigra (granula iridica) protruding from the superior and inferior iris margins of some large herbivours (Mann, 1931; Walls, 1942), such as camels (Rahi et al., 1980) and horses (Miller & Murphy, 2016; Figs. 4D&E), has a similar effect.

3.1.2 Pupil dynamics

3.1.2.1 Monotremes

There are only a few studies of ocular structure in monotremes (e.g. Pettigrew et al., 1998), and nothing is known of relevance to pupil mobility other than that the pupils are circular and the iris contains a well-developed sphincter, but no dilator (Walls, 1942). However, the presence of a sphincter does not necessarily imply pupil mobility as it may serve merely to maintain pupil shape (Section 2).

3.1.2.2 Marsupials

The PLR of marsupials is species dependent (Arrese et al., 2000; Arrese, 2002). The circular pupils of the strictly diurnal numbat and the nocturnal bilby are fixed, and the vertically oval pupil of the mainly nocturnal honey possum constricts only slightly on illumination, and the response is relatively slow, with a latency of 600msec and needing 4.8secs to reach maximal constriction. The circular pupil of the burrowing bettong constricts more fully, reaching an area 32% that of the fully dilated pupil, with a latency of 200msec and maximal constriction taking 1.7secs.

The largest pupillary constriction among marsupials is shown by the circular pupil of the arrhythmic fat-tailed dunnart, whose constricted pupil is extremely small, with an area only around 2% that of the dilated pupil. The response is also rapid, with a latency of less than 200msec and its extensive constriction is completed in only 1.6secs.

Thus, in marsupials the range and speed of the PLR is related to the range of light levels normally encountered by the animal. A species such as the dunnart, which can be active at both day and night, and may experience rapid changes in light level while hunting and avoiding predators during the day, would benefit from a rapid and extensive PLR. The other marsupials, on the other hand, normally experience more constant light levels, and would gain little from a highly mobile pupil.

3.1.2.3 Placentals

3.1.2.3.1 Primates

Primates are grouped into the strepsirrhines (lemurs, galagos, pottos and lorises) and haplorrhini (monkeys, apes and tarsirs). While vertically elongated pupils occur in a number of strepsirrhines in high light levels (Walls, 1942; Mann, 1931; Malmström & Kröger, 2006; Beltran et al., 2007), the pupils of 'higher' primates are circular at all levels of illumination.

For the reasons outlined in section 1, more is known about the pupil of humans than any other animal, but only a brief outline is given here as many reviews are available. Although not the most recent, perhaps the most informative source on the human pupil is the classic work by Loewenfeld (1993).

The adult human pupil changes in diameter from about 8mm when fully dilated to around 2mm when maximally constricted. Thus, the fully constricted pupil has an area about 6% of the dilated one, reducing the amount of light impinging of the retina by a factor of 16. As is common to most animals, pupil size and response latency decrease in brighter light (Figs. 5&6). The latency in humans ranges bewteen 180-500msec, depending principally on light intensity, but also influenced, for example, by the completeness of the proceeding dark adaptation, the spectral quality of the light, the location and extent of the retina stimulated, and the age of the person (Loewenfeld, 1993). During prolonged increases in light level, the pupil after its initial contraction redilates to varying degrees (Fig. 5D). In response to dim light this redilation is rapid and may be complete, while following exposure to higher light levels it proceeds more slowly and is only partial.

Most characteristics of the PLR of another simian, the rhesus macaque, are very similar to those of humans (Gamlin et al., 1998; Pong & Fuchs, 2000; Clarke et al., 2003), with, for example, latency and area decreasing and speed increasing as a function of light intensity. The major differences are that the latency of the macaque response is up to 100msec shorter than for humans and the response is faster. This may indicate a more ‘active relaxation’ of the dilator muscle in the monkey than in humans (Gamlin et al., 1998), or that the muscle physiology of these animals is simply faster than in humans.

Although detailed PLR dynamics are not available for many primates, it is clear that nocturnal species which are also occasionally active during the day, such as tarsirs and strepsirrhines, would benefit from extensive pupil movements. Consequently, their dilated pupils are often almost as wide as their enlarged eyes, but in light constrict to small oval or circular apertures (Walls, 1942; Wolin & Massopust, 1967; Pariente, 1979), resulting in a larger range of pupillary area than occurs in strictly diurnal species.

3.1.2.3.2 Rodentia

The most studied rodent pupils are those of mice who, due to their genetic versatility, are frequently used as a model for mammalian ocular physiology and pathology, and their PLR can be monitored to assess retinal function (e.g. Lucas et al., 2003; MacLaren et al., 2006; Perganta et al., 2013). As expected, the amplitude of contraction of the mouse pupil is a function of stimulus intensity, and the latency of the response to bright light is around 250msec (Grozdanic et al., 2003). In response to high light levels, the mouse pupil routinely constricts to about 5% of its dilated area (Lucas et al., 2001; Hattar et al., 2003; Maclaren et al., 2006; Ouk et al., 2016; Fig. 21).

Pupil constriction in rats, in comparison to mice, has a slightly longer latency (299msec), and in response to the same light level constricts less (Grozdanic et al., 2002), although comparable fully constricted areas to the mouse (4%) are possible (Lau et al., 1992).

Most work on hamster pupils involves the non-retinally mediated response of the isolated iris (Bito & Turansky, 1975; Suzuki et al., 1991; Section 6). However, the PLR of intact animals, in comparison to rats, is slower and in response to the same light level the pupil constricts less (Lau et al., 1992). Constriction in response to bright light to about 9% of the dilated pupil area, is achieved within 6-8secs, although areas of less than 1% of the dark adapted area do occur (Hut et al., 2008).

Although no detailed dynamic information is available concerning light-driven pupil responses in other rodents, the pupils of, for example, guinea pigs (Ostrin et al., 2014) and grey squirrels (McBrien et al., 1993) can be contracted and dilated by pharmacological agents.

3.1.2.3.3 Ungulata

Given the very characteristic, horizontally rectangular, shape of the pupil of many ungulates such as horses and sheep (Fig. 4D), it is perhaps suprising that there are no detailed studies of the pupil dynamics for any members of this group.

The horse's eye is one of the largest among terrestrial vertebrates. Consequently, the pupil dilated by either drugs (Mughannam et al., 1999; Davis et al., 2003) or low levels of illumination (Roth et al., 2008) is correspondingly large, with an area six times greater than that of humans (Miller & Murphy, 2016). In low light levels the dilated equine pupil is circular and in normal daylight takes on its familiar rectangular shape (Fig. 4D). However, in very high light levels the superior corpora nigra may reach the inferior iris, dividing the pupil into two small apertures (Miller & Murphy, 2016) (Fig. 4E). Although Walls (1942) states that the horse shows only slight pupil mobility, it appears the total excursion of the equine pupil is in fact greater than that of humans, although the rate of change in area is relatively slow (Miller & Murphy, 2016).

The size of the sheep pupil, like that of presumably most ungulates, depends on degree of ambient illumination (Seggie et al., 1989). Although the range of pupil movements in most ungulates is unclear, what seems certain is that their horizontally oblong or circular pupils do not close down as much as the slit-like pupils of animals such as cats (Section 3.1.2.3.5; Fig. 4B). The difference in the ability of slit and rectangular or circular pupils to constrict is a function of the arrangement of their iris sphincter muscles (Fig. 2), and is discussed in section 9.2.1.

3.1.2.3.4 Cetacea

This group of aquatic mammals, which encompasses whales, dolphins and porpoises, are closely related to even-toed ungulates (Artiodactyla). Pupillary area in the bottle-nosed dolphin depends on the level of illumination, and when normalised to the area of the maximally dilated pupil is very similar to that of humans at comparable illumination (Dawson et al., 1979). Maximal constriction takes 9-10secs and half maximal constriction is reached in about 1-1.8secs, depending on light intensity.

3.1.2.3.5 Carnivora

The basic dynamics of the cat PLR are similar to those of humans having, for example, a comparable latency (200-300msec) and pupil area decreasing with increasing luminance (Lowenstein et al., 1953; Lowenstein, 1954; Watanabe et al., 1990; Oh et al., 1995; Thompson et al., 2010; Fig. 7). However, humans and cats differ widely in their range of pupil movements. This is because the circular fully dilated feline pupil has an area of ca. 120mm^2, which is around three times as large as the human pupil, while the constricted vertical slit pupil of the cat is smaller than the human one (Wilcox & Barlow, 1975; Hammond & Mouat, 1985). Thus, the cat pupil changes in area from light to dark by a factor of around 135 (Section 9.2.1 for discussion).

Not all carnivores have constricted slit pupils. The pupils of dogs and big cats, for example, remain circular at all light levels. Consequently, changes in pupillary area in these species are relatively modest. For example, in one study the diameter of the dog pupil in low light levels was 8.3mm, which reduced to 5.7mm on illumination (Grozdanic et al., 2007). Thus, the constricted pupil area was still around half that of the dilated pupil. In most respects the dynamics of the dog pupil response are similar to humans, amplitude and velocity increasing and latency decreasing in brighter light (Whiting et al., 2013). The response latency of the dog pupil is also similar to most other mammals, ranging between ca. 133-381msec (Grozdanic et al., 2007; Whiting et al., 2013; Kim et al., 2015; Yeh et al., 2017).

As in marsupials (Section 3.1.2.2), the range of pupillary movements in different species of pinniped is related to the range of lighting conditions the animal normally experiences throughout the day. The Northern elephant seal routinely dives to depths in excess of 500m and therefore experiences a wide range of light intensities. Consequently, it has a very large circular pupil in darkness, which in bright lightly constricts to a small slit, whose area is only 0.2% of the area of its dilated pupil, representing an area change by a factor of 469. In contrast, in harbor seals and California sea lions, whose dives rarely exceed 100m, and who therefore experience lesser changes in light levels, the constricted pupils are wider slits that cause a lesser reduction in area to 1.4% and 3.8% of the dark adapted pupil area, respectively (Levenson & Schusterman, 1997). Such extensive pupillary movements contribute to the faster rate of dark adaptation and higher sensitivity in pinnipeds compared to man (Levenson & Schusterman, 1999).

3.2 Bird pupil responses

Although there are around 10,000 species of living birds, the pupils of few have been examined in detail. The limited available evidence indicates that bird pupil shape and the PLR are remarkably conservative when compared to the variability present in other groups of animals.

3.2.1 Pupil shape

In all but three species of bird, the pupil remains circular at all light levels (Mann, 1931). The exceptions are the adult black skimmer and the king and emperor penguins. Although, like other birds, these three species have large circular pupils in low lights levels, in daylight the pupils of the skimmer become a vertical slit (Zusi & Bridge, 1981), while those of the penguins become square pinholes (Martin, 1999; Lind et al., 2008).

3.2.2 Pupil dynamics

The first avian PLR to be quantified was that of the pigeon (Gundlach, 1934), whose pupil fully constricted on illumination before the human pupil in the same lighting had even begun to do so. This extreme rapidity of pupillary constriction has since been confirmed for all birds studied (pigeons – Lowenstein & Loewenfeld, 1959; Alexandridis, 1967a; chickens - Barbur et al., 2002; Moayed et al 2012: Owls - Bishop & Stark, 1965; Oliphant et al., 1983; Schaeffel & Wagner, 1992). Latencies to a single light flash are species specific (Kallähn, 2014) but are around 50msec, and maximum constriction is reached within about 100-150msec. Under comparable conditions humans have a longer latency (230msec) and maximal contraction is not reached until much later (800msec) (e.g. Barbur et al., 2002; Fig. 8). Consequently, the pupils of chickens (Barbur et al., 2002) and pigeons (Alexandridis, 1967a) are able to respond at higher frequencies than those of humans (Lowenstein & Loewenfeld, 1959; Loewenfeld, 1993).

The fast dynamics of the bird PLR are easily explained by the presence of striated muscle in the avian iris, compared to the exclusive use of smooth muscle in the irises of mammals, fish and amphibia (Section 2). Pupil dilation following the cessation of a light stimulus, as in other vertebrates, is significantly slower than constriction (Lowenstein & Loewenfeld, 1959; Bishop & Stark, 1965; Alexandridis, 1967a; Oliphant et al., 1983; Moayed et al., 2012) and is similar to that in mammals (Loewenfeld, 1993). This may be because the dilator muscle of birds, unlike the sphincter, often has a significant smooth muscle component (Section 2).

The fast PLR of birds may be an adaptation to the rapid changes in light levels that might be experienced during flight. This may explain why, perhaps rather bizarrely, it has been suggested that the degree to which the pupil of a racing pigeon can constrict on light exposure may be an indicator of its quality as a racing animal (Nyitrai et al., 2010).

As in most animals, light-driven changes in bird pupil areas are related, at least to some extent, to the level of the illumination (Alexandridis, 1967a; Schaeffel et al., 1986; Barbur et al., 2002; Lind et al., 2008; Figs. 6&7). The sensitivity of contraction depends on both species and age. Diurnal parrots, for example require more light for pupil constriction than nocturnal owls (Fig. 7), presumably because their retinae are less sensitive and need to maximise photon capture at higher light levels (Lind et al., 2008). The pupils of young chickens constrict in response to higher light levels compared to those of older animals (Scaheffel et al., 1986), suggesting decreased retinal sensitivity in younger animals.

With the exception of diving birds (Section 8.3.2) and the 3 species with non-circular pupils (Section 3.2.1), the PLR of most birds appear relatively modest compared to those of mammals (Section 3.1.2), but are comparable to those of reptiles (Section 3.3.2) and amphibia (Section 3.4.2.2) with circular pupils. While many mammals constrict their pupils to just a few percent of their fully dilated area in bright light, the pupils of parrots and owls never constrict to more than 30% of their dark adapted area (Lind et al., 2008; Fig. 7). Similarly, while the pupils of humans closed to 19% of their fully dilated area in response to illumination, those of chickens only reduced their area to 58% of their dark adapted area (Barbur et al., 2002; Fig. 6).

Although the pupils of birds do not alter in area in response to simple changes in illumination as much as those of some other animals, they can respond well to more specific stimuli such as the colour red (Barbur et al 2002; Section 8.2; Fig. 8). They also undergo considerable excursions in the absence of significant changes in light level, even prompting the suggestion that the bird pupil may sometimes be subject to voluntary control (Section 8.2).

3.3 Reptilian pupil responses

Extant reptiles comprise four main orders; Testudines (turtles, terrapins and tortoises), Sphenodontia (tuatara), Squamata (lizards and snakes), and Crocodylia (crocodiles, gavials, caimans, and alligators). However, extant reptiles are not a natural (monophyletic) group because some, namely crocodylians (and perhaps testudines), are more closely related to birds than they are to other extant reptiles. In modern classification, there is no formal name for the non-monophyletic group comprising reptiles but not birds. Reptilia is sometimes used as a name for a monophyletic group comprising ‘reptiles’ and birds (e.g. Simões & Gower, 2017). However, for the purposes of this review, birds are discussed in another section (Section 3.2).

3.3.1 Pupil shape

In all reptiles, the dilated pupil is close to circular (Walls, 1942; Mann, 1931; Werner, 1967), but on illumination pupil shape varies widely. It ranges from circular in all testudines (Mann, 1931; Granda et al., 1995; Rival et al., 2015), some snakes (Mann, 1931; Werner, 1970; Brischoux et al., 2010), and many lizards (Mann, 1931;

New et al., 2012), to a narrow vertical slit in many snakes (Mann, 1931; Walls, 1942; Werner, 1967; Brischoux et al., 2010), crocodylians (Mann, 1931; Allen & Neill, 1950; Walls, 1942), and in sphenodontia (Mann, 1931). Horizontally slit pupils are less common in reptiles, but occur, for example, in some tree snakes (Mann, 1931; Heath et al., 1969). Additionally, in some lizards, the edges of the iris are not regular, resulting in a variety of unusual constricted pupil shapes (Mann, 1931).

One of the strangest pupil shapes occurs in geckos. A few diurnal species have circular, possibly largely immobile, pupils (Underwood, 1954; Werner, 1967, 1969). Most geckos, however, are nocturnal or crepuscular and their pupils constrict in the light to become vertical slits. In some species, the edges of the slit are straight and the constricted pupil has a single elongated aperture. In others, however, the pupil edges are scalloped so that when the pupil constricts the irregular edges of the iris overlap, forming four, vertically aligned pinholes, each with a diameter of 0.1mm or less (Mann, 1931; Underwood, 1951, 1954; Denton, 1956; Werner; 1969, 1972; Fig. 9). The function of such multiple pupillary apertures is discussed in section 9.3. The difference between the dilated and constricted areas in such a pupil is a factor of around 100-300, larger eyes showing a greater difference between light and dark adapted pupil size (Denton, 1956; Courjon, 1977; Frankenberg, 1979; Roth et al., 2009). The sizes of the two pupils of a gecko vary independently (Section 4.3) and, especially at lower light intensities, appear to be under voluntary control (Denton, 1956; Werner, 1972), allowing them to perhaps have a role in the regulation of aggressive interactions (Section 8.2).

Members of all reptilian orders have the ability to rotate their eyes so that eye position is maintained at different degrees of pitch of the head (Munro, 1949, 1950; Allen & Neill, 1950; Heath et. al., 1969). This is especially apparent in species with vertical slit pupils, but is also true, but less easy to see, for animals with circular pupils. The utility of such eye movements is discussed in section 9.2.3.

3.3.2 Pupil dynamics

Rather surprisingly, although pupil shape has been widely discussed for various reptilian species and extensive pupil movements have been noted in many species (Steinach, 1890), information on timecourses and the extent of constriction are only available for two species.

The pupil of the green iguana constricts rapidly (latency 70-170msec) and both the latency and amplitude of the response depend on light intensity (Krastel & Alexandridis, 1972). However, the most comprehensively studied reptilian pupil, that of the red-eared slider turtle, is very different. Compared to the iguana, its PLR is very sluggish, constriction taking about 5mins (Dearworth et al., 2009).

The short latency of the iguana PLR is similar to that of birds (Section 3.2.2), and can easily be explained by the striated nature of its iris muscles (Section 2). Since the turtle also has striated iris muscles, its slow response needs explanation and may be related to a greater reliance on the slow kinetics of melanopsin-based phototransduction to initiate the PLR in this species (Section 5.2.3.1).

The total change in area of the turtle pupil is not as great as in some animals, the pupil in bright white light only constricting to around 30-50% of its fully dark adapted area (Granda et al., 1995; Dearworth et al., 2009, 2010; Sipe et al., 2011). The pupil of a lizard constricts even less, reaching only 70% of its dark adapted area in bright light (New et al., 2012), although the pupils of some snakes contract to a greater degree (Werner, 1970) and, as discussed above (Section 3.3.1; Fig. 9), the gecko's pupil shows extreme adaptability.

Although most animals with mobile pupils constrict them in higher light levels, some semi-aquatic snakes, surprisingly, decrease pupillary area when underwater, where light levels are reduced compared to on land (Schaeffel & de Queiroz, 1990; Fontenot, 2008). This apparent anomaly may be related to the requirements of amphibious vision (Section 8.3.2).

3.4 Amphibian pupil responses

Extant amphibia, of which there are around 7000 species, all belong to the subclass Lissamphibia and can be divided into three orders; the Anura (frogs and toads), the Caudata (salamanders), and the Gymnophiona (caecilians) (Pyron & Wiens, 2011).

3.4.1 Caecilians

Caecilians lead a largely subterranean existence. However, although their eyes are much reduced in size compared to those of other amphibia, and covered by a layer of skin or bone, they are not, as their Latin name might suggest, blind. Structurally, their eyes have all the main components of those of other vertebrates; their retina is well-developed and contains a functional visual pigment (Mohun et al., 2010).

However, as predictable from their life style, their eyes are used primarily for the detection of light intensity and direction, to guide phototactic behaviours, and perhaps detect object movement, rather than detailed image formation (Wake, 1985; Himstedt, 1995; Mohun & Wilkinson, 2015). The reduced nature of the iris and the lack of iris muscles makes changes in pupil area unlikely.

3.4.2 Anura & caudata

In contrast to caecilians, anura and caudata undergo significant pupil movements.

3.4.2.1 Pupil shape

The dilated pupil in the vast majority of amphibia, as in most vertebrates, is close to circular. However, the constricted pupil shape is variable, ranging from circular in, for example, African clawed frogs, to vertically or horizontally elongated, as in midwife toads and ranid frogs, respectively. In some anura, the constricted pupil has also been variously described as; pear-shaped, heart-shaped, and club-shaped with a variety of notches in the pupil margin related to the position of the hyaloid vessels during development (Mann, 1931; Fig. 10). Several amphibia also have projections from the dorsal edge of the pupil, usually called umbracula (Mann, 1931; Kruger et al., 2013), equivalent to the opercula of other animals (Section 9.1).

Aspects of amphibian ocular morphology, including pupil shape, are important taxonomic markers (Glaw & Vences, 1997) and pupil shape has sometimes been related to specific ecological variables. It is often assumed, for example, that vertically elongated pupils are associated with an arboreal lifestyle. However, while vertical pupils are common to all phyllomedusine frogs (Tyler & Davies, 1978), a genus of Central and South American tree frogs, among mantellid frogs both arboreal and terrestrial species have horizontally elongated pupils (Amat et al., 2013). Similarly, a genus of African hyperoliid tree frog has a horizontally elongate pupil, while those of close relatives are vertical (Roedel et al., 2009). A reliable correlation between amphibian pupil shape and lifestyle remains elusive.

3.4.2.2 Pupil dynamics

Most work on amphibian pupil dynamics relates to the response of the isolated iris (Section 6), and there are very few detailed timecourses of the PLRs of intact amphibia. The first appears to be a single curve shown by Lowenstein & Loewenfeld (1959), who note that the frog's pupil reacts sluggishly, compared to man.

The most detailed descriptions of the PLRs of intact amphibia are for ranid frogs (Cornell & Hailman, 1984) and two species of newt (Henning et al., 1991). The newts, in response to the highest light intensity used, constricted to 44% and 51% of their dark adapted area respectively, while the frog reached a level of about 35%. A potential drawback of these studies was that animals were pharmacologically immobilised, potentially affecting the pupil response. However, my own unpublished observations on unrestrained intact animals confirm the work on immobilised animals. In response to bright white light (3.39×10^3 μW/cm^2), the pupils of unrestrained common frogs (*Rana temporaria*) constricted to 42% of their fully dilated area in darkness (16 responses from 4 animals; +/- 6% sd). Complete constriction took between 8-30secs and the t_{50} was on average 3.7 (+/- 1.3)secs. Similarly, green toads (*Bufo viridis*) constricted to 35-40% in a similar timeframe.

Thus, most intact amphibia seem to be able to constrict their pupils to about 40% of their dark adapted area in response to bright light.

In both immobilised (Cornell & Hailman, 1984; Henning et al., 1991) and unrestrained (Fig. 11) animals, the degree of constriction is related to light intensity. In prolonged illumination the pupils of frogs (Cornell & Hailman, 1984; Fig. 11), but not newts (Henning et al., 1991), redilate to a certain degree.

Armstrong & Bell (1968) suggested aquatic amphibia have less of a pupil response than terrestrial species. Indeed, it has been reported that the sphincter muscle in the iris of the aquatic African clawed frog is poorly developed, and that its pupil does not change in size on illumination (Weale, 1956). However, although the response is less than in other amphibia, even this species shows a graded PLR to illumination (Fig. 12), constricting to an average area 70% (17 responses from 10 animals; +/- 11.8%) of that in the fully dilated pupil in response to bright illumination (3.39×10^3 $\mu W/cm^2$) with t_{50} occurring on average 4.7secs after the onset of illumination. Thus, for this one aquatic species at least, the response is indeed less than for the terrestrial species examined to date.

3.5 Fish pupil responses

Fish is a loosely and not consistently defined term, which encompasses a heterogeneous group of aquatic vertebrates that have gills throughout their lives and fins rather than limbs (Nelson, 1994). Only the two largest groupings, the cartilaginous elasmobranchs and the bony teleosts, will be considered here, as pupil data for other groups is sparse, although lungfish are known to show a degree of pupil mobility (Steinach, 1890; Walls, 1942; Bailes et al., 2007).

Teleost fish, which account for almost half of all vertebrate species, are unusual, as the vast majority have no significant pupil mobility. Living elasmobranchs can most conveniently be divided into the selachii (sharks) and the batoidea (skates, rays and sawfish). In contrast to teleosts, with the exception of deep-sea species (Kuchnow, 1971), the pupils of most elasmobranchs are highly mobile. Whether the pupils of sawfish are mobile is unknown (Wueringer, pers com).

3.5.1 Pupil shape

While dilated pupils of sharks are close to circular (Fig. 13A), constricted pupil shape varies from circular, to elliptical, to various orientations of slits. The fully constricted pupil of the swell shark, for example, consists of little more than a slit which, as in many other species (Franz, 1931; Young, 1933a; von Studnitz, 1933; Kuchnow, 1971), has a small pinhole at either end (Fig. 13B). Although it has frequently been suggested that nocturnal sharks have slit-like constricted pupils, while those of diurnal species are circular (Franz, 1905; Young, 1933a; Walls, 1942), there are exceptions to such a generalisation (Gilbert et al., 1981; McComb et al., 2009).

Many skates and rays are characterised by the growth of dorsal iris operculae during constriction (Bateson, 1890; Franz, 1905; Kuchnow, 1971; Kuchnow & Martin, 1972; Collin, 1988; Franz, 1931; Young, 1933a; Walls, 1942; Gruber & Cohen, 1978; Nicol, 1978; Sivak & Luer, 1991), resulting in a variety of pupil shapes, depending on the species and light level, including crescent moons and multiple pinholes (Figs. 14A&B).

The immobile pupils of most teleosts are circular, or nearly so, although some depart from circularity and possess aphakic spaces within, for example, teardrop-shaped pupils (Section 9.5). Although the dark adapted pupils of those few teleost species with mobile irises are also circular (Figs. 13C&E), their shape can be quite different when constricted. The pupil of the plainfin midshipman, for example, contracts in the light to two small, almost independent, pinholes (Fig. 13D; Walls, 1942; Douglas et al., 1998). The constricted pupil of the armoured catfish, on the other hand, displays a dorsal operculum, similar to that observed in skates and rays, forming a crescent-shaped light adapted aperture (Fig. 13F; Douglas et al., 2002). Other substrate living teleosts, such as flatfish (Bateson, 1890; Walls, 1942), mudskippers (Munk, 1970), and scorpaeniformes (Figs. 14C&D), also have dorsal intrusions into the pupil (Section 9.1 for a discussion of the possible function of such operculae).

3.5.2 Pupil dynamics

3.5.2.1 Sharks

As first suggested by Franz (1905, 1906), the pupils of nocturnal and diurnal sharks behave differently (Young, 1933a; Kuchnow 1970, 1971).

Nocturnal species have a rather slow PLR, taking up to 15mins to constrict fully to about 2-20% of the dilated area and show no signs of redilation in continued illumination (Young, 1933a; Gruber, 1967; Kuchnow, 1971). Fig. 15, for example, shows the timecourse of constriction of a dark adapted nocturnal swell shark to prolonged bright illumination. The pupil steadily constricts over a period of several minutes to a horizontal slit tilted at 20º to the body axis connecting 2 small pinholes with an aperture of around 2% of the dark adapted area (Fig. 13B; Douglas et al., 1998).

In diurnal species, on the other hand, although the extent of light-evoked constriction is similar to that of nocturnal species, the response is much faster, often occurring within a minute or less, and in continued illumination the pupils re-open to some extent following initial constriction (Franz, 1906; Young, 1933a; Kuchnow & Gilbert, 1967; Kuchnow, 1970, 1971; Gilbert et al., 1981). As in various species of bird (3.2.2), the pupils of diurnal sharks have a higher threshold for pupil constriction than those of nocturnal species (Kuchnow, 1970).

3.5.2.2 Skates & rays

Like nocturnal sharks, the PLRs of skates and rays are slow, taking between 5-15mins to constrict fully (Nicol, 1978; Kuchnow, 1971). The decrease in area on constriction of their opercular pupils (Figs. 14A&B) varies considerably with species, with the area of the light adapted pupil ranging between 85-27% of the fully dilated pupil area (Nicol, 1978; Kuchnow, 1971), although it would not be surprising if the pupils of other species constricted to a greater degree.

3.5.2 3 Teleosts

Although very limited pupil responses have been elicited in both intact teleosts and isolated eyes by either electrical stimulation (Beer, 1894; Nilsson, 1980; Somiya, 1987; Fujimoto et al., 1995) or changes in ambient illumination (Brown-Séquard, 1859; Steinach, 1890; Studnitz, 1932a) in several species, such movements are very small and unlikely to be of any physiological significance, and many may be the result of the protruding lens displacing the iris during accommodative movements.

Extensive pupillary excursions in response to light have been described in only a few bony fish. Qualitatively, highly contractile pupils have been noted in eels (Steinach, 1890, 1892; Studnitz, 1932a; Brown-Séquard, 1847a&b, 1859; Magnus, 1899; Guth, 1901; Seliger, 1962), stargazers and monkfish (Beer, 1894; Young 1931, 1933b), oyster toadfish *(*Rubin & Nolte, 1981), and pearlfish (Walls, 1942). Preliminary data indicated that some flatfish also have mobile pupils (Beer, 1894; Bateson, 1890; Steinach, 1890). The pupil of the sole contracts to 20% of its dilated area within 10-20secs of light exposure, while other species such as brill, turbot, plaice, scaldback and flounder also constrict, but to a lesser degree (Douglas, unpubl). The pupils of various members of the scorpaeniformes probably also have mobile pupils (Figs. 14C&D).

Detailed timecourses have only been published for the PLRs of two teleosts.

The plainfin midshipman shows pupillary constriction that is as fast and extensive as that of man (Douglas et al., 1998). Half maximal contraction is reached 0.4-0.8secs after light onset, with the fully constricted pupil having an area around 5% of the dilated pupil (Fig. 15). The degree of constriction depends on the level of illumination and, as in the stargazer (Young, 1931), in prolonged illumination at all but the highest intensities, the pupil redilates somewhat after its initial constriction (Fig. 16).

The pupils of armoured suckermouth catfish also display extensive pupil responses, contracting to an area about 30% of that of the dilated pupil, although these movements occur much more slowly than in the midshipman, full constriction taking 35-40mins (Douglas et al., 2002; Fig. 17). The catfish also shows no signs of an increase in pupil area during prolonged illumination (Fig. 17). Both the slow timecourse of the response and the lack of redilation in the catfish are similar to the responses of nocturnal elasmobranchs (Kuchnow, 1971; Douglas et al., 1998; see above).

It is noteworthy that the few teleosts that do have mobile pupils, with the exception of the eel and pearlfish, are bottom-dwelling species that try to conceal themselves in the substrate. The functional significance of this will be discussed in section 7.2.

3.5.2.3.1 Why do most teleosts not have mobile pupils?

When looking for a proximate cause for the lack of a mobile pupil in most teleosts, one must ask whether there is something about the teleost eye that prevents iris mobility. The most obvious thing would be a lack of iris muscles. However, most teleosts have an iris sphincter muscle and sometimes a dilator (Grynfeltt, 1910; Section 2; Fig. 3).

Another explanation for the lack of pupil mobility may be that, as noted elsewhere (Section 8.3.2), the cornea is optically ineffective underwater so the lenses of teleost fish have to be optically more powerful than those of non-aquatic animals and are therefore spherical in most species. The large size of the lens means it protrudes through the pupil, effectively blocking it and possibly preventing changes in its area.

Such an argument receives some support from other aquatic species. The pupils of elasmobranchs are generally highly mobile (Sections 3.5.2.1 & 3.5.2.2), and their lenses are usually more flattened than those of teleosts (Sivak, 1990, 1991). Similarly, the armoured catfish has a subspherrical lens and a mobile pupil (Douglas et al., 2002). However, this argument is weakened by the fact that other teleosts also have non-spherical lenses (Sivak, 1990), yet do not have mobile pupils. Furthermore, dolphins (Rivamonte, 2009) and other cetacea (West et al., 1991), have both round lenses and mobile pupils (Dawson et al., 1979).

It has been suggested that the ultimate cause for a lack of pupil mobility in teleosts is that retinal light and dark adaptation in these animals involves retinomotor movements (for reviews, Burnside and Nagle, 1983; Wagner et al., 1992; Burnside and Kingsmith, 2010). Changes in pupillary area and the positional shifts of photoreceptors and retinal pigment epithelial melanin were thought to have “a mutual relationship” (Duke-Elder, 1958), with pupillary mechanisms representing the more “advanced” form of adaptation (Walls, 1942; Ali, 1975). Thus, teleost fish might have no need for mobile pupils as they display retinomotor movements. However, such a view is untenable as many animals, including amphibia, elasmobranchs (Gilbert et al., 1981), eels (Studnitz, 1932a), and plainfin midshipman (Douglas et al., 1998), have both extensive retinomotor movements and significant pupillary responses.

In truth, neither the proximate nor the ultimate causes for of the lack of pupillary responses in the majority of teleost have been resolved.

3.6 Cepahlopod pupil responses

There are around 800 living species of cephalopod divided into 2 subclasses; the Nautiloidea and Coleoidea. The nautiloids are often referred to as living fossils as they have changed little for millennia, and the more 'advanced' coleoids diverged from ancestors not dissimilar to modern day nautiloides about 420 million years ago. While all extant nautiloides belong to a single order with only a few species, living coleoides are more diverse and include squid, octopus and cuttlefish (Allcock et al., 2015). While nautiloides have 'primitive' pinhole eyes, coleoids have eyes that are optically similar to those of vertebrates (Muntz, 1999).

3.6.1 Pupil shape

The dark adapted pupils of all cephalopods are large and frequently close to circular. On light exposure, however, the pupil can take on a variety of more irregular forms. In octopus, for example, the constricted pupil frequently becomes a horizontal rectangle (Magnus, 1902; Weel & Thore, 1936; Douglas et al., 2005; Talbot & Marshall, 2011; Fig. 18A), often in the brightest light consisting of little more than 2 small pinholes at the end of an elongated aperture (Fig. 18B). In squid, on the other hand, the constricted pupil is often crescent-shaped (McCormick & Cohen, 2012; Talbot & Marshall, 2011; Chung & Marshall, 2017; Fig. 18C), but can also be either a horizontal (Talbot & Marshall, 2010) or a vertical (Matsui et al., 2016) slit.

The oddest pupil shape is that of the cuttlefish, which can assume the shape of an extended or flattened W when constricted (Muntz, 1977; Douglas et al., 2005; Talbot & Marshall, 2011; Mäthger et al., 2013; Chung & Marshall, 2017; Fig. 18E). It seems different regions of this complex pupil are controlled locally with, for example, only the back or the front of the W dilating when the animals fixate objects of interest, such as approaching divers, in different directions (Talbot & Marshall, 2010).

Octopus have a statocyst-oculomotor system similar to the vestibulo-ocular system of vertebrates (Budelmann & Young, 1984). Thus, whatever the orientation of the animal, the slit pupil always remains horizontal (Wells, 1960). On removal of the statocysts, the position of the pupil reflects the position of the head, which is determined by how the animal is sitting on the substrate, and its ability to perform visual discriminations is impaired (Wells, 1960). Reptiles (Section 3.3.1) and other vertebrates (Section 9.2.3) show similar rotatory eye movements.

3.6.2. Pupil dynamics

It has been known for over 100 years that both major groups of cephalopods have pupils whose size varies depending on light intensity (Beer, 1897; Bateson, 1890; Magnus, 1902; Weel & Thore, 1936), although accurate timecourses of the responses did not become available until much later.

The PLRs of all cephalopods studied to date are extensive, the pupil area usually reducing, depending on the species, to less than 5-20% of its fully dilated area in bright light, and often being too small to measure accurately. However, the speed of the response varies between different groups of cephalopods.

In *Nautilus,* the pupil response is comparatively sluggish; full constriction to bright light occuring in around 90secs (Hurley et al., 1978). The pupils of coleoid cephalopods respond more quickly, although earlier estimates of their dynamics considerably underestimated the speed of constriction (Muntz, 1977).

The most rapid PLRs have been recorded in two species of cephalopod in the order sepiidae, t_{50} occurring in on average 320msec (Douglas et al., 2005; Fig. 19). Only birds have similarly rapid responses (Section 3.2.2).

Pupil constriction in the Atlantic brief squid (McCormick & Cohen, 2012) and the Japanese flying squid in response to bright light is only slightly slower than in cuttlefish. Octopoda, such as the curled octopus, show similar PLRs (Douglas et al., 2005; Fig. 19). Perhaps surprisingly, in the Southern reef squid even embryonic stages show limited light-induced pupil closure, and some individuals fully constrict their pupil when aged only 2 days (Bozzano et al., 2009).

Even more surprisingly, a deepsea octopus, *Japetella diaphana*, also has a PLR, although less extensive and more sluggish than that of other coleoids. In response to light the pupil constricts to about 8% of its dilated area in approximately 15secs (t_{50} 8.5secs) (Fig. 20). Adult *Japetella a*re usually found at depths of around 700-950m and there is no evidence of diel vertical migration (Young, 1978). 1000m is the lower limit to which visually usable sunlight can penetrate the clearest oceans (Denton, 1990), and in most waters sunlight disappears at considerably shallower depths. It is therefore surprising that *Japetella diaphana*, a species thought to live at depths at which there is little or no sunlight, has a PLR at all. As bioluminescence, the only other source of illumination at such depths, is unlikely to be bright enough to cause pupil constriction, the PLR of this species remains a mystery.

Cephalopod pupil size is not only influenced by the ambient illumination, but also reflects the ‘arousal’ of the animal. Such light-independent movements are discussed further in section 8.2.

4. Consensual pupil responses

In humans, light shone into only one eye evokes a similar contraction of the pupil in both the stimulated and unstimulated eye (Fig. 5A-C). These are known as the direct and consensual responses, respectively. When both eyes are illuminated simultaneously, the pupil constricts more than when either eye alone is stimulated. While the direct response depends on both the classical central neural circuits (Section 5), as well as any intrinsic iris response (Section 6), central pathways alone will drive the consensual response.

Early studies suggested that consensual responses are restricted to ‘higher’ mammals (Steinach, 1890; Harris, 1904). Although this view is still widespread (e.g. Lowenfeld, 1993), there is ample evidence that consensual pupil responses do in fact occur among ‘lower’ mammals, as well as in non-mammalian species, although the direct response is always larger than the consensual one in these animals. Such differences between the direct and consensual response can usefully be expressed as a percentage (degree of consensual/direct constriction).

No response in the unilluminated eye following unilateral illumination or identical responses in both eye, are almost certainly a true indication for the absence or presence of a consensual response. However, a lesser response in the unilluminated eye must be treated with some caution, as it might be the result of two artefacts; the ‘unilluminated’ eye was either stimulated by scattered light or light reached it via transcranial illumination. The latter is a particular problem in birds, where large eyes are separated by only a thin bony septum (Steinach, 1890; Levine, 1955; Schaeffel et al., 1986).

4.1 Mammals

Early work suggested that ‘lower’ mammals such as ungulates, rodents and rabbits did not have consensual pupil responses, while in ‘higher’ mammals such as dogs, cats, lions and primates, the stimulated and unstimulated eye behaved identically (Steinach, 1890; Harris, 1904). However, this work was mainly qualitative and we now know the situation is not this clear cut.

Following unilateral illumination in humans and other primates the responses of the stimulated and unstimulated eyes are indeed identical, or nearly so (Lowenstein & Friedman, 1942; Carpenter & Pierson, 1973; Smith et al., 1979; Loewenfeld, 1993; Clarke et al., 2003). There has been a report that in the rhesus macaque the consensual response is both significantly slower and smaller than the direct response (Pong & Fuchs, 2000), but this may be the result of experimental error (Clarke et al., 2003). The consensual light response in mice also has the same amplitude and latency as the direct response, although its velocity may be somewhat slower (Grozdanic et al., 2003; Hussain et al., 2009).

In dogs (Grozdanic et al., 2007) and cats (Lowenstein et al., 1953; Lowenstein, 1954) the consensual response is slightly reduced (ca. 95%) compared to that of the illuminated eye. In rats, the amplitude of the consensual response is reduced even further to 76-78% of the direct response (Trejo et al., 1989; Grozdanic et al., 2002), and only a small consensual response has been reported in the horse (Harris, 1904). The same author suggested that in rabbits only the stimulated eye contracts, although later studies indicate the rabbit too has a degree of consensual response (Inoue, 1980).

Thus, most, if not all, mammals have a consensual pupil response, whose similarity to the direct response varies depending on the species.

4.2 Birds

True consensual pupil responses (i.e. those not caused by stray light) are generally assumed to be absent in birds (Steinach, 1890; Harris, 1904; Levine, 1955; Gregory & Hopkins, 1974; Bishop & Stark, 1965; Schaeffel et al., 1986; Schaeffel & Wagner, 1992). However, two studies cast at least some doubt on such a generalisation. Intact chickens (Schaeffel et al., 1986) and owls (*Tyto alba* - Schaeffel & Wagner, 1992; *Bulbo bulbo* & *Strix ulula* – Steinach, 1890), like other birds, have been reported to have pupils that behave independently. However, other studies in which the optic nerve of one eye was severed have come to a different conclusion. In both chickens (Li & Howland, 1999), and a different species of owl (*Athene noctua*; Berlucchi & Strata, 1964), illumination of the operated eye did not induce constriction of its pupil, as the afferent limb of the reflex arc had been cut. It also did not induce any constriction in the contralateral eye, showing the absence of any transcranial illumination. However, illumination of the unoperated eye did result in some pupil constriction in the operated eye of both species. This suggests that chickens, and at least one species of owl, do have a degree of neuronal consensual response.

Interestingly, bird pupils often change in area in the absence of alterations in the ambient illumination, responding, for example, to sounds and vocalisation, and possibly have an element of voluntary control (Sections 3.2.2 & 8.2). While, simple light-driven pupil responses may not be consensual, such more centrally controlled pupil responses are similar in both eyes (Harris, 1904; Gregory & Hopkins, 1974).

4.3 Reptiles

Early reports on 15 species suggested the pupils of all reptiles reacted independently to light (Steinach, 1890). The lack of a consensual response was subsequently confirmed for geckos (Denton, 1956; Werner, 1972), Vietnamese leaf turtles (Henze et al., 2004), and iguanas (Krastel & Alexandridis, 1972). However, careful examination shows the red-eared slider turtle does have a consensual response, although the unstimulated eye constricts to a lesser degree (35%) than the stimulated one (Dearworth et al., 2010).

4.4 Amphibia

In four species of salamander, the pupils of the two eyes behaved independently (Steinach, 1890; Henning et al., 1991). However, although early studies suggested anura also lack consensual pupillary responses (Steinach 1890; Harris, 1904; von Studnitz, 1932b), at least two species of frog on unilateral illumination showed pupil contraction in the unstimulated eye, albeit slower and of lower amplitude than in the stimulated eye (Campenhausen, 1963).

4.5 Fish

Among elasmobranchs, rays appear to have a consensual response (Bateson, 1890; Franz, 1931), whereas sharks do not (Bateson, 1890; Steinach, 1890; Franz 1931; Studnitz, 1933; Kuchnow, 1971). Only a few teleost fish have mobile pupils (Section 3.5.2.3). In the plainfin midshipman both eyes constrict when only one is illuminated, but the unstimulated eye responds to a lesser degree (70%; Douglas et al., 1998). Other teleosts with mobile pupils lack any form of consensual response (Nilsson, 1980; Steinach, 1890; Young, 1931).

4.6 Cephalopods

Among cephalopods the situation appears equally varied. Illumination of only one eye in *Nautilus* results in constriction of both eyes to the same degree, although the unilluminated eye tends to redilate somewhat, which the stimulated eye does not (Hurley et al., 1978). In coleoid cephalopods, on the other hand, the two pupils are usually said to react independently (Magnus, 1902; Weel & Thore, 1936; Hanlon & Messenger, 1988), although this has only been quantitatively investigated in three species. In cuttlefish and curled octopus (Douglas et al., 2005) the unstimulated eye shows no response to unilateral illumination. In Atlantic brief squid**,** however, the unstimulated eye does contract, although it is less sensitive and contracts to a lesser degree (29%) than the stimulated eye (McCormick & Cohen, 2012).

4.7 Relationship between consensuality, binocular vision and decussation at the optic chiasm

Steinach (1890), after an extensive survey, concluded that the pupils of all vertebrates except ‘higher’ mammals responded independently to illumination. Interestingly, following a similar study, Harris (1904) reached exactly the same conclusion, although he seemed unaware of the extensive work of his predecessor. Both authors assumed that only the optic nerve fibres of mammals partially decussated at the optic chiasm, while those of other species crossed completely, explaining why only mammals had consensual pupil responses. However, such a view is too simplistic.

Firstly, although consensual responses are more widespread in mammals than in other vertebrates, as is clear from the preceding sections, they do occur in all vertebrate classes. Secondly, although the view that only mammals have uncrossed fibres at the optic chiasm is still widespread (e.g. Leff, 2004), it is known that some members of all vertebrate classes do in fact have varying degrees of uncrossed fibres projecting ipsilaterally (Ebbesson, 1984; Ward et al., 1995; Jeffery, 2001). The degree of crossing over at the optic chiasm cannot be easily related to any single variable, such as a particular mode of life or taxonomic position (Ward et al., 1995).

There is, however, a (loose) correlation between the extent of the consensual pupil response and the position of the eyes. Thus, animals with frontal eyes and a large binocular field of view often have a well-developed consensual pupil response, while it is less pronounced in animals with more lateral eyes. Within mammals, for example, primates have large horizontal binocular fields of around 120º and near identical direct and consensual pupil responses. Carnivores, such as cats and dogs, also have large binocular overlaps (Heesy, 2004) and only slightly reduced consensual pupil responses. Rats have more laterally placed eyes (binocular field 85º; Hughes, 1979) and have a significantly reduced consensual response , while rabbits, whose eyes are even more lateral (binocular field 24º; Hughes & Vaney, 1982), have only a small consensual response. Similarly, the eyes of most birds point laterally, with only a small horizontal binocular field limited to 20º-30º (Martin, 2007, 2009), and mostly lack consensual pupil responses. However, there are exceptions to such a general correlation. The mouse, for example, has lateral eyes (binocular field ca. 40º; Drager, 1978), yet the direct and consensual pupil response are almost identical. Conversely, owls are the only birds with frontal eyes and extensive binocular fields (Martin 2007), and consequently exhibit true binocular stereopsis (Willigen et al., 1998), yet all but one study suggest their pupils behave independently.

4.8 Function of the consensual pupil response

In the laboratory, the consensual pupil response is investigated by exposing one eye to illumination while keeping the other in darkness. However, in nature animals will never be subjected to such uneven illumination, and most of the time differences in illumination between the two eyes, if present at all, will only be slight. The question must therefore be asked, what is the purpose of a consensual pupil response?

The preceding section (Section 4.7) suggests that animals with larger binocular fields tend to have a greater degree of consensuality in their pupil response. Since such animals often use stereoscopic cues to judge distance (Collett & Harkness, 1982), they may benefit from having a similar pupil size for both eyes, as differences in pupil size could result in differences in image quality in the two eyes, which would impair binocular fusion. Another advantage of a consensual pupil response in animals with large visual binocular fields might be that the uneven illumination of the two retinae resulting from significantly different pupil sizes, might give an illusory depth component to lateral motion (Pulfrich effect).

Lateral-eyed animals, however, may be disadvantaged by identical pupil responses in their two eyes, as these might be seeing quite different things. In fact, the two eyes of animals with large monocular fields behave independently in ways other than their PLR. For example, while in primates and some carnivorous mammals with forward facing eyes, the movements of the two eyes are perfectly coordinated, in some lateral-eyed non-mammalian vertebrates, such as the chameleon and a few fish, they move totally independently (Land, 2015 for review). Similarly, animals with frontal eyes and true stereoscopic vision, such as primates (Bishop & Pettigrew, 1986) and owls (Schaeffel & Wagner, 1992; Glasser et al., 1997), always show binocularly coupled accommodation. Lateral-eyed reptiles (Schmid et al., 1992; Ott et al., 1998; Henze et al., 2004) and birds (Glasser et al., 1997; Schaeffel et al., 1986), on the other hand, can accommodate independently in their two eyes (Ott, 2006 for review).

Thus, animals with lateral eyes and large monocular fields of view will not only view different scenes with their two eyes, their eyes may also behave independently to examine objects within those scenes. In fact, there is ample evidence that in some species the two eyes actually perform different functions. Lateralisation at both a structural and functional level is widespread in both vertebrates (Bisazza et al., 1998) and cephalopods (Byrne et al., 2002), and either one eye or the other can be used preferentially for a specific behaviour.

Given the independence of visual physiology and even function in the two eyes of animals with large monocular fields, it is no surprise that the pupils should behave independently too. In fact such animals could be disadvantaged if the pupils were always the same size. Imagine a small ground feeding, lateral-eyed, lizard with one eye focussed on a close potential prey item and the other eye keeping a wary look out for a distant approaching predator, such as a raptor. The eye examining the prey object might benefit from a dilated pupil, as it needs to assess its distance using a monocular cue such as its accommodative state, which would be impaired by the large depth of field of a constricted pupil (Section 8.3.1). The other eye viewing the sky, on the other hand, may benefit from a constricted pupil that reduces glare.

5. Neural pathways underlying retinally-mediated pupil responses

The muscles of the iris can be made to contract in two ways; direct action of light on the muscle fibres and by release of neurotransmitters from postganglionic fibres of the autonomic nervous system. The relative importance of these two forms of control is species specific and only nervous control is described in this section. Direct muscle photosensitivity is discussed elsewhere (Section 6).

Autonomic control of iris muscles is performed by sympathetic and parasympathetic reflex arcs, which are remarkably conserved in all vertebrate groups (Nilsson, 1994; Neuhuber & Schrödl, 2011; McDougal & Gamlin, 2015 for reviews). The degree of retinal illumination is detected by retinal photoreceptors, and specialised retinal ganglion cells carry the afferent signals away from the eye within the optic nerve. Central components of the afferent elements of the parasympathetic pathway are only known in detail for mammals and birds, and involve areas of the pretectum projecting to the accessory oculomotor nucleus, most commonly referred to as the Edinger-Westphal nucleus (EWN), in the rostral mesencephalon. Less is known about the central projections of the afferent limb of the sympathetic pathway.

In all vertebrates, efferent preganglionic parasympathetic fibres arise from the EWN and travel within the 3rd cranial nerve, the oculomotor, to synapse in the ciliary ganglion (CG), from where postganglionic fibres enter the globe and run in the suprachoroid towards the iris. Preganglionic fibres forming the beginning of the efferent limb of the sympathetic reflex arc arise from species-specific segments of the spinal cord and project to cranial sympathetic chain ganglia, such as the superior cervical ganglion in mammals and birds. Although sympathetic chain ganglia are present in elasmobranchs, there is apparently no sympathetic innervation of the eye (Young, 1933a). In all other species, postganglionic sympathetic fibres run from the chain ganglia to innervate the iris muscles. As the distance from the chain ganglia to the effector muscle is relatively long, this route is often a circuitous one.

Although all vertebrates possess similar autonomic reflex arcs controlling the iris muscles, there are significant differences between classes and species, which will be outlined below.

5.1 Retinal photoreceptors underlying the pupil response

Traditionally the eye is thought of as providing a detailed optical image of the world through light acting on rods and cones at low and high light levels respectively. These image-forming photoreceptors were until recently considered the only trigger for light-evoked, retinally-mediated, pupillary constriction (Loewenfeld, 1993). However, during the last 20 years it has become apparent that the eye has another, non-rod non-cone, photoreceptor controlling many of the non-image-forming functions of the eye, such as providing input to the body's endogenous clocks to synchronise an animal's behavioural, physiological, and biochemical rhythms to the daily light/dark cycle.

The properties of the photoreceptors underlying the diverse functions of the eye are very different. While image-forming photoreceptors, especially cones, respond quickly and briefly, their responses diminishing after a few seconds in order to provide spatial and temporal detail, a photoreceptor for non-image-forming vison needs to measure overall light levels over a longer period of time, and requires a more sustained response. It is therefore not surprising, although it undoubtedly came as a great shock to many, that light-mediated responses, such as the resetting of circadian rhythms (Freedman et al., 1999) and the regulation of pineal melatonin levels (Lucas et al., 1999), persisted in mice with neither rods nor cones, implying the existence of another type of retinal photoreceptor. This has now been identified as a class of intrinsically-photosensitive retinal ganglion cells (ipRGCs) containing the visual pigment melanopsin (Berson et al., 2002; Hattar et al., 2002), which comprise around 1% of ganglion cells in the mammalian retina (Bailes & Lucas, 2010; Lucas, 2013 for reviews).

These ipRCGs are not a homogenous class of cell, and in mice, several different morphological subtypes project to diverse regions in the brain, and have many different functions (Ecker et al., 2010).

As the PLR is primarily a response to overall light levels, it is not surprising that ipRGCs have also been implicated in its control. Thus, like other non-image-forming processes, near normal pupil response occur in mice lacking rods and cones (Lucas et al., 2001; Fig. 21), but are lost once the ipRGCs are also eliminated (Hattar et al., 2003; Panda et al., 2003). The involvement of ipRGCs in the pupil response has now been shown to be widespread among other mammals too, including primates (Gamlin et al., 2007; Young & Kimura, 2008; McDougal & Gamlin, 2010) and dogs (Yeh et al., 2017).

In mammals, rods, cones and ipRGCs all contribute to the PLR, their relative contributions depending on stimulus intensity, wavelength and time since light onset (Lall et al., 2010; Markwell et al., 2010; Lucas et al., 2014; McDougal & Gamlin, 2015 for reviews). Most simply, while rods and cones underlie the initial rapid pupillary closure at all but the highest intensities, the ipRGCs are responsible for sustained pupillary closure, especially at higher intensities of illumination, compensating for the rapidly adapting traditional photoreceptors.

Melanopsin-containing ipRGCs also play a role in the pupil responses of non-mammalian vertebrates. The slower pupil response of turtles compared to man (Section 3.3.2) might, for example, be explained by a more prominent role for melanopsin in this species (Section 5.2.3.1). Inner retinal photoreceptors also contribute to the PLR of chickens (Valdez et al., 2009), and melanopsin is involved in the intrinsic iris photosensitivity of amphibia (Section 6). It seems likely that melanopsin will be involved, to varying degrees, in the pupil responses of most vertebrates.

5.2 Postreceptoral neural pathways controlling pupil size

In the following sections, the principal innervation of the iris muscles will be outlined. Thus, in mammals for example, the parasympathetically induced contraction of the sphincter muscle is emphasised. However, it is likely that iris muscles in most species in fact have dual and opposing autonomic innervation, so that the mammalian sphincter is also inhibited by sympathetic innervation, although this is sparse compared to the excitatory parasympathetic control (see references in Armstrong & Bell, 1968; Nilsson, 1980; Neuhuber & Schrödl, 2011; McDougal & Gamlin, 2015).

Furthermore, the iris is also innervated by neurons in the ophthalmic portion of the trigeminal ganglion of birds and mammals and the profundus ganglion of fish, amphibia and reptiles. Such fibres can release peptides in response to, for example, inflammation, noxious stimuli, or changes in temperature, which then influence the muscles of the iris as well as performing their ‘normal’ sensory functions (see references in Neuhuber & Schrödl, 2011; McDouglal & Gamlin, 2015).

Neither dual autonomic innervation nor control of iris muscles by trigeminal neurons is discussed further here.

Details of innervation have mostly been elucidated either pharmacologically or by lesioning/stimulating specific neural pathways. Barr (1989) reviews much early comparative information on the innervation of iris muscles, while Neuhuber & Schrödl (2011) give a more recent review.

5.2.1 Mammals

For obvious reasons (Section 1), most is known about the neural pathways underlying pupil constriction and dilation in primates, and these have been extensively reviewed (e.g. see references in McDougal & Gamlin, 2015; Fig. 22). Only these are briefly described here, as the pathways are broadly similar for all mammals.

5.2.1.1 Innervation of the sphincter

The output of all retinal photoreceptors involved in the pupil response is conducted by the axons of the ipRGCs within the optic nerve, through the optic chiasm, and along the optic tract. Although the majority of tract fibres end in the lateral geniculate nucleus of the thalamus, most of the ipRGC axons leave the optic tract before it reaches the thalamus, at the superior brachium, and some synapse in the OPN. As all retinal ganglion cells, including those projecting to the pretectum, undergo partial decussation at the optic chiasm, the OPN receives input from the temporal retina of the ipsilateral eye and the nasal retina of the contralateral eye.

There have been suggestions that different ipRGC subtypes differentially innervate the OPN (Baver et al., 2008). In mice, M1 ipRCGs project to the outer shell of the

OPN, and are most probably the main drivers of the PLR, while the core of the OPN receives input from other classes of ipRGCs as well as non-melanopsin ganglion cells, which may or may not be involved in controlling the pupil (Ecker et al., 2010).

From the OPN information is relayed by short neurons that synapse bilaterally on preganglionic parasympathetic neurons in the EWN of the midbrain (Kozicz et al., 2011). Efferent signals pass along parasympathetic fibres within the oculomotor (3rd cranial) nerve to the orbit, where they synapse in the CG. Postganglionic fibres travel in the short ciliary nerves, through the choroid, to the sphincter pupillae, where they release acetylcholine which, via muscarinic receptors (largely, but not exclusively, M_3), causes the sphincter to contract and reduce the size of the pupil.

5.2.1.2 Innervation of the dilator

Pupillary dilation is brought about by lessening the parasympathetic input to the sphincter, and by sympathetic activation of the dilator muscle. Sympathetic preganglionic fibres arise from the intermediolateral nucleus in the 8th cervical to the 2nd thoracic spinal segments, an area known as the ciliospinal center of Budge (and Waller), and travel in the sympathetic trunk to the superior cervical ganglion. Postganglionic neurons travel up the neck next to the internal carotid artery as the internal carotid nerve. At the level of the cavernous sinus, the nerve breaks up to form an interweaving network of fibres, the carotid plexus, around the carotid artery. Some of the axons from this plexus form the sympathetic root of the CG, pass through the CG without synapsing and, mostly travelling in the short ciliary nerves, innervate the iris dilator. Other postganglionic sympathetic fibres reach the dilator in long ciliary nerves, which are branches of the nasociliary nerve (not shown in Fig.

22). These sympathetic fibres travel within the choroid and release noradrenaline onto the dilator, which, acting on α_1 receptors, causes pupillary area to increase.

5.2.2 Birds

5.2.2.1 Innervation of the sphincter

The neural pathway underlying the PLR has been thoroughly described for the pigeon and is very similar to that outlined for humans above (Section 5.2.1.1). A small subset of large retinal ganglion cells project to an area of the contralateral pretectum (area pretectalis), which when stimulated causes pupil constriction. There are no ipsilateral projections from the retina to this area. From here fibres reach the contralateral EWN and send preganglionic oculomotor nerve parasympathetic fibres to the CG, which gives rises to postganglionic neurons that innervate the iris sphincter muscle (Gamlin et al., 1984).

In mammals, anti-muscarinic drugs such as atropine cause pupil dilation. In adult birds, however, such drugs usually have little effect, but those that block nicotinic acetylcholine receptors, as in turtles (Section 5.2.3.1), are effective in causing pupil dilation (Campbell & Smith, 1962; Mikaelian et al., 1994; Ramer et al., 1996; Loerzel et al., 2002; Barsotti et al., 2010a&b, 2012; Petritz et al., 2016). The muscarinic action of acetylcholine on the iris sphincter of mammals, but its nicotinic action in birds and turtles, is easily explained by these muscles being smooth in mammals and striated in birds and reptiles (Section 2). Consequently, in developing chicks, when iris muscles are smooth, the receptors on the sphincter are muscarinic, and nicotinic receptors only appear in adults when most muscle becomes striated (Pilar et al., 1987).

5.2.2.2 Innervation of the dilator

Sympathetic control of the avian dilator is derived from preganglionic spinal neurons located in the lowermost cervical and uppermost thoracic segments that, as in mammals, project to the superior cervical ganglion from where postganglionic fibres reach the muscle (Kirby et al., 1978; Neuhuber & Schrödl, 2011).

While in the pigeon the dilator muscle has been described as vestigial or absent (Pilar et al., 1987; Gamlin et al., 1984), in other species, although not as well developed as the sphincter, it is readily apparent (Zenker & Krammer, 1967; van Oehme, 1969; Nishida & Sears, 1970; Oliphant et al., 1983; Scapolo et al., 1988; Pilar et al., 1987; Dieterich et al., 1988). Its control appears variable, perhaps because it can consist of both striated and smooth components (Section 2). Thus, while some studies indicate cholinergic control (Pilar et al., 1987), and show little effect of adrenergic drugs on pupil size (Campbell & Smith, 1962; Zenker & Krammer, 1967), others suggest adrenergic control of the dilator (Nishida & Sears, 1970; Kirby et al., 1978) and, for example, find phenylephrine to cause dilation (Loerzel et al., 2002).

5.2.3 Reptiles

The neural pathways underlying pupil responses have been examined in some detail for the red-eared slider turtle. Broadly speaking they are similar to those described for mammals (Section 5.2.1) and birds (Section 5.2.2).

5.2.3.1 Innervation of the sphincter

Pupil constriction involves parasympathetic elements of the 3rd cranial nerve synapsing in the CG and the postganglionic action of short ciliary nerves releasing acetylcholine onto the sphincter muscle. Thus, stimulation of both the 3rd nerve and short ciliary nerves, as in alligators (Iske, 1929), results in a decrease in pupil area (Dearworth et al., 2009) and acetylcholine antagonists block constriction (Dearworth et al., 2007).

As noted in section 5.2.1.1, while in mammals contraction of the iris sphincter muscle is brought about by the action of acetylcholine on muscarinic receptors, in the turtle and birds the acetylcholine acts on nicotinic receptors (Dearworth et al., 2007). Interestingly, early studies on another reptile, the alligator, gave somewhat different results, suggesting the control of the sphincter was similar to that in mammals involving the muscarinic action of acetylcholine (Iske, 1929). However, the alligator sphincter muscle has both smooth and striated components (Reger, 1966), potentially explaining the variation in control of the reptilian iris sphincter muscle (Dearworth et al., 2007).

In comparison to mammals, pupillary constriction in the turtle is relatively slow, taking up to 5mins (Dearworth et al., 2009; see Section 3.3.2). However, direct stimulation of the efferent pathway results in much faster pupillary constriction (Dearworth et al., 2009), suggesting the cause of the sluggish PLR of turtles is to be found within the afferent part of the reflex arc. In the turtle, pupillary constriction may, for example, be more reliant than mammals on melanopsin-containing ipRGCs, whose dynamics are slow (Dearworth et al., 2011; Section 5.1).

5.2.3.2 Innervation of the dilator

In the red-eared slider turtle, pupil dilation, as in mammals, is mediated via the action of noradrenaline on α_1 receptors (Dearworth & Cooper, 2008), suggesting the presence of sympathetic innervation of a dilator muscle similar to that described in sea turtles (Brudenall et al., 2008).

5.2.4 Amphibia

Although direct iris photosensitivity (Section 6) is perhaps the principle way of contracting amphibian iris sphincter muscles, there is ample evidence that their iris muscles also receive extensive autonomic innervation.

5.2.4.1 Innervation of iris muscles in caudata

The innervation of the iris of salamanders has been little studied. In the Spanish ribbed newt, section of the 3rd cranial nerve leads to slower and smaller PLRs (Henning et al., 1991). Furthermore, in this species and fire salamanders a prectecal area that projects to the CG via the oculomotor nerve has been identified as being involved in pupillary constriction (Henning & Himstedt, 1994), suggesting parasympathetic control of the iris sphincter muscle. The sluggish nature of the dark response in these species (Henning & Himstedt, 1994), as well as morphological data for the Japanese common newt (Okamoto, 1988), suggests caudata do not have an iris dilator muscle. Since both catecholamines and acetylcholinesterase were localised to the pupillary margin of the newt iris and two types of varicosities were described within nerve endings, which in other species have been linked to cholinergic and adrenergic innervation, it is possible the iris sphincter receives a dual innervation, as has been suggested for some anura (Section 5.2.4.2) (Okamoto, 1988).

5.2.4.2 Innervation of iris muscles in anura

Pupil constriction in anura is perhaps solely the result of the direct action of light on the sphincter muscle (Section 6). Although it was initially proposed this muscle could be made to contract by stimulation of cholinergic parasympathetic fibres within the 3rd cranial nerve (Armstrong & Bell, 1968), this could not be confirmed (Morris, 1976). Despite some contradictory evidence (e.g. Studnitz, 1932b; Kotsuka & Naito, 1960), most data indicate that in both frogs (Ducret and Kogo, 1931; Hafter, 1932) and toads (Armstrong & Bell, 1968; Morris, 1976; Rubin & Nolte, 1984) β-adrenergic sympathetic innervation, arising from the 2nd, 3rd or 4th spinal root (Morris, 1976), results in pupil dilation. As there is no structural evidence for a dilator muscle in either Northern leopard frogs (Nolte & Pointner, 1975) or cane toads (Armstrong & Bell, 1968), pupil dilation is generally assumed to be brought about by sympathetic inhibition of the sphincter muscle. However, toads might in fact have myoepithelial fibres that could function as a dilator (Rubin et al., 1986). A clear unified picture of anuran iris innervation is therefore yet to emerge.

5.2.5 Fish

While in mammals, birds, reptiles and amphibia the iris sphincter muscle is either primarily under parasympathetic control or receives no innervation, and the dilator muscle, when present, is primarily innervated by sympathetic fibres, in fish the control of these muscles is reversed.

5.2.5.1 Innervation of iris muscles in teleosts

In a variety of teleosts, the iris sphincter muscles are sympathetically innervated (Young, 1931&1933b; Nilsson, 1980; Somiya, 1987) and can be made to contract cholinergically &/or adrenergically. However, it is possible that the adrenergic responses are non-specific and the sympathetic innervation of the teleost iris sphincter muscle is cholinergic (Rubin & Nolte, 1981). The iris dilator muscle, when present, is under cholinergic parasympathetic control from fibres within the oculomotor nerve (Young, 1931, 1933b; Somiya, 1987). The often contradictory literature on the innervation of fish iris muscles is reviewed by Nilsson (1994).

5.2.5.2 Innervation of iris muscles in elasmobranchs

Little is known about the control of elasmobranch iris muscles. As in teleosts, the dilator muscle is parasympathetically controlled by fibres within the 3rd cranial nerve projecting to the CG (Young, 1933a; Kuchnow, 1971), from where (possibly cholinergic) fibres act on the dilator muscle. It has been suggested that the sphincter receives no innervation and responds only to direct illumination (Young, 1933a; Section 6). However, the iris sphincter muscles of some elasmobranchs have been shown to have nerve terminals on them (Kuchnow & Martin, 1970), suggesting a degree of nervous control of this muscle, at least in some species.

5.2.6 Cephalopods

Although it is probable that cephalopods, like most vertebrates, possess both iris sphincter and dilator muscles (Magnus, 1902), the presence of a dilator has yet to be clearly demonstrated anatomically (Froesch, 1973). The fast rate of cephalopod pupil dilation, however, is strongly suggestive of the presence of such a muscle.

Little is known about the neural pathways underlying the cephalopod pupil response. Early observations regarding its central components in octopus (Magnus, 1902) were later questioned by Weel & Thore (1936). However, a region between the posterior pedal and ventral magnocellular lobes, which receives direct input from the optic lobe, has been identified as being involved in the control of pupil diameter (Budelmann & Young, 1984). Three ganglionated nerves, when stimulated, affect the size of the pupil; two (n. ophthalmicus superior posterior & n. oph. inferior) causing constriction and one (n. oph. superior medialis) resulting in dilation. It is also known that pupil constriction in *Sepia* results from the application of acetylcholine (Chichery & Chanelet, 1972), although in other cephalopods atropine does not block constriction (Beer, 1897).

6. Intrinsic iris photosensitivity

Light activated pupillary constriction is traditionally thought of as a centrally-mediated reflex, in which illumination of retinal photoreceptors, by way of the optic nerve, triggers motor neurons leading to contraction of the iris sphincter muscles (Section 5). However, it has been known for over 150 years that the pupils of some amphibia and fish constrict on illumination even in the absence of retinal input (Brown-Séquard, 1847a&b, 1859; Steinach, 1892; Magnus, 1899; Guth, 1901; Franz, 1906). Since then, numerous studies using, intact eyes removed from the head, isolated irises or iris muscles, intact eyes within the body following optic nerve section, or small spots of light directed only at the irises of intact animals, have shown that the irises of most, and perhaps all, amphibia, are directly photosensitive (Weale, 1956; Campenhausen, 1963; Glaus-Most, 1969; Barr, 1989 for reviews and references listed below). Significant intrinsic iris photosensitivity has also been reported in other fish (Franz, 1906, 1931; Young, 1933a; Seliger, 1962; Kuchnow, 1971; Rubin & Nolte, 1981; Douglas et al., 1998), several mammals (Bito & Turansky, 1975; Zucker & Nolte, 1978; Suzuki et al., 1991; Lau et al., 1992; Krivoshik & Barr, 2000; Xue et al., 2011; Semo et al., 2014; Vugler et al., 2015), a reptile (Sipe et al., 2011), and embryonic chicks (Pilar et al., 1987; Tu et al., 2004; Valdez et al., 2009).

However, intrinsic iris photosensitivity, while obviously widespread, is not universal in animals with mobile pupils. While some, mainly nocturnal/crepuscular, mammals, for example, appear to have intrinsically photosensitive irises (see references above), diurnal species, including primates, do not (Xue et al., 2011). Similarly, while in some teleost fish the isolated iris responds to light, in the stargazer such changes in pupil area cease following disruption of the optic nerve (Young, 1931, 1933b), and in the gecko illumination of only the iris is ineffective in eliciting pupillary closure (Denton, 1956). Although Barr (1989) goes so far as to suggest that in all but a very few animals the isolated iris is capable of some contraction, it may not always be physiologically significant.

Barr & Alpern (1963) provided the first detailed timecourse for pupillary constriction in an isolated amphibian iris in an unidentified species of frog, showing an average latent period of under a second with maximum tension developing in ca. 4-5secs. Later studies show similar dynamics for the isolated irises of toads (Armstrong & Bell, 1968), frogs (Glaus-Most, 1969; Kargacin & Detwiler, 1985), and axolotls (Barr, 1988). Just like the PLR following nervous stimulation, the intrinsic pupil response is related to light intensity (Fig. 23).

The pupil responses of isolated irises and intact animals are sometimes very similar (Studnitz 1932a &1933; Steinach, 1892), which led to the suggestion that the pupil responses in these animals are entirely the result of direct iris photosensitivity. Furthermore, in sharks the sphincter muscle seems to receive no innervation and contract solely in response to its own photosensitivity (Young, 1933a; Section 5.2.5.2). However, often the response of the isolated iris is significantly slower and less extensive than that of the intact eye (Campenhausen, 1963; Bito & Turansky, 1975; Henning et al., 1991; Lau et al., 1992; Douglas et al., 1998; Sipe et al., 2011). There is also ample evidence that the autonomic nervous system has a significant role to play in the pupil responses of all animals (Section 5), and the existence of a consensual pupil light response in many animals (Section 4) could not be explained by intrinsic iris photosensitivity. Thus, the complete pupil response usually requires some retinal input.

Structurally, intrinsically photosensitive irises appear little different to those of other species, containing no specialised photoreceptive cells or organelles (Bell, 1965; Armstrong & Bell, 1968; Nolte & Pointner, 1975; Zucker & Nolte, 1981; Rubin et al., 1986). It is therefore assumed that the sarcolemma of the iris sphincter contains the visual pigment. Early evidence, based on the similarity of the action spectrum of the isolated iris response and the absorption spectrum of the rod visual pigment (Magnus, 1899; Seliger, 1962; Barr & Alpern, 1963; Bito & Turansky, 1975; Barr, 1988), and the localisation of rhodopsin and elements of its phototransduction cascade in the iris (Blaustein & Dewey, 1979; Ghosh et al., 2004; Xue et al., 2011), indicated that it might underlie intrinsic iris photosensitivity. Such a suggestion is not unreasonable, as embryologically the iris muscles have a common developmental origin with the retina.

However, the relatively recent discovery of the plethora of novel visual pigments (Foster & Hankins, 2002; Davies et al., 2015), both within and outside the retina, requires a reappraisal of the role of rod visual pigments in intrinsic iris photosensitivity. One of these novel opsins, melanopsin, which underlies many non-image-forming visual responses, including part of the retinally-mediated pupil response (Section 5.1), has an absorption spectrum very similar to that of rod visual pigments, with maximum sensitivity around 480nm (Lucas et al., 2001; Bailes & Lucas, 2010). It has also been localised in the iris of amphibia (Provencio et al., 1998), turtles (Cheng et al., 2017), and mice (Xue et al., 2011; Vugler et al., 2015). Furthermore, the isolated iris response of mice disappears in melanospin knockout animals (Xue et al., 2011; Semo et al., 2014; Vugler et al., 2015), and the action spectrum of the intrinsic pupil response closely matches the absorption spectrum of melanopsin (Xue et al., 2011). However, the intrinsic iris response is unaffected in rhodopsin knockout mice (Xue et al., 2011). It thus seems likely, that in many species, melanospin, rather than rhodopsin, underlies the intrinsic photosensitivity of the iris sphincter muscle.

Interestingly, the non-opsin based cryptochrome has been shown to take on the role of the visual pigment in embryonic chick irises (Tu et al., 2004), although it is not involved in mice (Xue et al., 2011). It also cannot be ruled out that, as has been suggested in turtles (Sipe et al., 2011), more than a single pigment type might underlie intrinsic iris photosensitivity.

The signalling pathways linking opsin-based visual pigment activation to iris sphincter contraction are beginning to be elucidated (Barr, 1989: Krivoshik & Barr, 2000; Xue et al., 2011). Either rhodopsin or melanopsin is coupled, via a G-protein, to a typical smooth muscle phosphorylation contraction cascade involving phospholipase C (Krivoshik & Barr, 2000; Xue et al., 2011) and the release of intracellular calcium (Barr & Alpern, 1963; Bito & Turansky, 1975; Zucker & Nolte, 1978: Rubin & Nolte, 1984; Kargacin & Detwiler, 1985; Barr & Gu, 1986, 1987; Barr, 1989; Suzuki et al., 1991; Krivoshik & Barr, 2000; Xue et al., 2011). Unlike in retinal photoreceptors, cyclic nucleotides appear not to be involved directly in the transduction process (Rubin & Nolte, 1984, 1986; Kargacin & Detwiler, 1985), although they may have a modulatory role (Barr, 1989).

In many animals, there are thus two distinct pathways leading to contraction of the iris sphincter muscle; a reflex arc involving retinal photoreceptors and the brain and intrinsic photosensitivity of the iris sphincter muscle itself. However, at least in mice, there may be a third way of triggering pupil constriction; a local intraocular reflex involving the retina. The pupil response of animals whose optic nerve has been destroyed is influenced by cholinergic transmission from ipRGCs that project from the peripheral retina and ciliary body directly to the iris (Semo et al., 2014; Schmidt et al., 2014). Retinal rods, but not cones, also have a role to play in the pupil response of isolated mouse eyes (Vugler et al., 2015).

The centrally-mediated component of pupil constriction is so well established that an obvious question is, what is the purpose of additional intrinsic iris photosensitivity?

Most simply perhaps, an intrinsic iris response allows sustained contraction of the pupil once it has constricted and the retina receives reduced illumination. The retinally-mediated component of the PLR is presumably required so that the state of adaptation of the retina can be assessed. Furthermore, as the PLR is more than a simple response to overall light levels that serves to regulate retinal illumination, and can respond to quite complex stimuli (Sections 7&8), central involvement in its control is required.

7. Function of changes in pupil area related primarily to light intensity

7.1 The pupil as a way of optimising visual performance in different light levels

The difference between a cloudy night and a bright sunlit day can expose an animal to a range of light levels of over 10 log units during a 24hr period, which far exceeds the dynamic range of any one photoreceptor. Although the eyes of vertebrates are generally optimised for vision in either high or low light levels, most maintain some vision at all times by switching between two differentially sensitive photoreceptors; the rods which optimise sensitivity in low light levels, and the less sensitive cones underlying high spatial acuity in brighter light. The switch from rod to cone-based vision and the adjustment of their sensitivity involves a number of complex biochemical and neurobiological retinal processes (Perlman & Normann, 1998; Lamb & Pugh, 2004).

Such retinal light and dark adaptation is usually accompanied by changes in pupillary area. As the iris acts as an aperture stop, photon capture by the retina will be enhanced by a large pupil, easily explaining the dilated pupil in low light levels. Animals at high light levels, however, will benefit from smaller pupils as all lenses suffer from optical imperfections. For example, spherical aberration is caused by light going through the periphery of the lens being focussed closer to it than more central rays (Section 9.1.1; Fig. 25). A large aperture would thus reduce image quality, as most of the lens is used to form the image. Large pupils may further reduce image quality, as they result in a decreased depth of field. Thus, a constricted pupil enhances image quality by reducing the amount of spherical aberration and increasing the depth of field, although if it is too small diffraction may become a problem (McDougal & Gamlin, 2015). Although, pupillary constriction probably serves to reduce spherical aberration in many species, it may not do so in all (Section 9.1.1).

If an animal lived in an environment where the level of illumination did not fluctuate, it would not need any means of light or dark adaptation and its pupil would probably be fixed. The greater the variation in light level experienced by an animal the more extensive any adaptive mechanisms need to be. As will be described in a later section (9.2.1), nocturnal animals that nonetheless are sometimes active during the day, and therefore experience a wide range of light levels, often have pupil shapes, such as slits, that allow a greater change in pupil area than the circular pupils of strictly diurnal or nocturnal species. Marsupials that live in relatively constant illumination have pupils that change little, if at all, while species that experience a wider range of light levels show a greater range of pupil areas (Section 3.1.2.2). Nocturnal primates (Section 3.1.2.3.1) and geckos (Section 3.3.1) have a greater range of pupil sizes than strictly diurnal species. Similarly, the greatest pupillary excursions among pinnipeds are seen in deeper diving species, which experience the greatest range of light levels (Section 3.1.2.3.5). Also, while most birds show relatively modest light-evoked pupil responses, pupillary area altering retinal illumination by a factor of only around 3-4 (Section 3.2.2), the pupil of the King Penguin, which dives to dimly-lit depths to feed, can change in area by a factor of 300 (Martin, 1999; Section 3.2.1). Thus, the extent of the PLR is greater in animals that experience a wide range of illumination.

Although large changes in pupil area are clearly possible, the variation in retinal illuminance resulting from most pupil responses is in fact fairly limited (1.2 log units in the case of humans; see Section 9.2.1), thus providing only a modest contribution to adjusting to the much wider range of light levels animals can be exposed to.

Although the pupil, especially a circular one, may not be able to compensate for anything like the whole range of light levels an animal might be exposed to, its advantage is that it is usually very rapid, while the other processes involved in light and dark adaptation, although more effective, often take several minutes. Thus, a mobile pupil allows the visual system to regain optimal sensitivity more rapidly by smoothing out fast changes in ambient light levels. It could, for example, reduce the amount of visual pigment bleached in bright light, thereby reducing the amount of regeneration that has to occur once the ambient illumination decreases, allowing a faster rate of dark adaptation.

Thus, changes in pupil area are part of a suite of changes involved in light and dark adaptation, and pupil diameter is continually adjusted to optimise visual performance in response to changing environmental lighting conditions and different visual tasks, balancing the conflicting demands of sensitivity and spatial acuity.

7.2 Camouflage

The blackness of the pupil, and its often regular circular outline, make the eye particularly visible. Sometimes, such as when the eye is used for social interactions (Section 8.2), such conspicuousness is clearly advantageous and the visibility of the pupil is further enhanced by the colouration of the sclera and iris. For example, determining where another animal is looking is important for certain forms of social interaction in some animals (Davidson et al., 2014), as it might, for example, indicate the location of an object of interest. In humans, the large white exposed sclera has been interpreted as an aid to determining gaze direction (Kobayashi & Kohshima, 2001).

However, its conspicuousness, its sensitivity and the reliance of many animals on vision, also make the eye particularly vulnerable to attack. Furthermore, it may at times be advantageous to conceal one’s direction of gaze, possibly accounting for the more pigmented scleras of non-human primates (Kobayashi & Kohshima, 2001). Cott (1940), in his classic text on animal camouflage, considered the eye inherently conspicuous and the most difficult of all organs to conceal.

Some animals therefore attempt to hide the eye using masking body patterns such as black stripes, or disguise the eye’s true location by using false eyes to misdirect an observer (Cott, 1940; Walls, 1942; Neudecker, 1989). Such patterning is particularly obvious in some teleost fish (Fig. 24), where the lack of eyelids and nictitating membranes makes ocular conspicuousness, as well as protection, a particular problem.

While such mechanisms for concealing the eye may be applicable in colourful reef fish, they are inappropriate for bottom-dwelling species that are trying to blend in with the substrate. While it is a relatively simple matter for them to match the colour and texture of the skin to the background, the eye, especially the pupil, is less easy to disguise.

This may explain why mobile pupils in teleost fish are largely confined to species that live on, or in, the substrate (Section 3.5.2.3). Pupillary constriction in higher light levels might serve to conceal the otherwise very prominent dark circular pupil, as the anterior surface of the iris usually matches the bodily pigmentation. In lower light levels, when potential predators and prey will be able to perceive less detail, the pupil can expand to increase the concealed animal's sensitivity.

Dorsal operculae (Fig. 14), which will conceal the eye from predators and prey viewing the hiding animal from above (Section 9.1), will aid crypsis in bottom dwelling fish. This will be further enhanced by disrupting the regular outline of the otherwise circular pupil with an operculum whose edge is serrated or feathered (Fig. 14).

Using pupillary constriction to conceal the eye, while perhaps most obvious in fish, need not be restricted to this group. The vertical slit pupils of snakes that are ambush predators (Brischoux et al., 2010; Section 9.2.3), and the multiple pinholes of the gecko pupil (Roth et al., 2009; Section 9.3; Fig. 9C), may serve a similar function, as they are less regular and have a reduced area in comparison to a single circular pupil.

8. Changes in pupil size not related to ambient light level

Perhaps the most obvious causes of changes in pupil diameter unrelated to light level are pathological (Loewenfeld, 1993), and result from interruptions in the neural pathways controlling pupillary responses (Section 5). Although the changes in pupil diameter related to pathology, and their usefulness in diagnosing neurological disease, have been the main drivers for pupil research (Section 1), this will not be discussed further in this section.

8.1 Rhythmic changes in pupil diameter

The human pupil undergoes slow rhythmic contractions in constant illumination, especially when sleepy, known as hippus or pupillary unrest (Loewenfeld, 1993; Fig. 5D). Similar contractions are observed in other mammals such as rhesus macaques (Pong & Fuchs, 2000), dogs (Whiting et al., 2013), and mice (McGinley et al., 2015) but not in, for example, dolphins (Dawson et al., 1979). Rhythmic variations in pupil size are also widespread in birds (Steinach, 1890; Alexandridis, 1967b; Raidal, 1997; Kallähn, 2014; Meekins et al., 2015) and cephalopods (Douglas et al., 2005) and have been reported after prolonged dark adaptation in turtles (Steinach, 1890; Granda et al., 1995). Respiration (Ohtsuka et al., 1988) and heart rate (Calcagnini et al., 2001) can also influence pupil size. Finally, the pupils of at least mice, humans and birds are subject to the influence of endogenous circadian clocks, and are thus influenced by the time of day (Owens et al., 2012; Münch et al., 2012; Valdez et al., 2015; Bonmati-Carrion et al., 2016).

8.2 Influence of ‘higher level processing’ on pupil size

In humans, there is ample evidence that the pupil is not controlled solely by the subcortical pathways outlined in section 5.2.1, and that higher level processing affects pupil size too. Such influences can be the result of both visual, as well as non-visual, neural activity. Although such changes in pupil size are usually not as large as those elicited by changes in light levels, they can be significant (Loewenfeld, 1993).

The human pupil, for example, responds to changes in colour, structure, and movement in the absence of net changes in total light flux (Barbur & Forsyth, 1986; Barbur et al., 1992; Barbur, 2004). The pupil is also affected by various physiological influences. Thus, pupillary diameter increases in times of stress responding, for example, to pain (Höfle et al., 2008), fear, and loud noises (Nunnally et al., 1967). It is also influenced by tiredness (Wilhelm et al., 1998) and physical activity (Ishigaki et al., 1991).

However, perhaps most surprisingly, pupil size is also influenced by factors that might be termed psychological. To give a few examples from a vast literature: Pupil diameter is increased when viewing emotionally arousing stimuli (Bradley et al., 2008). Classically, pictures of attractive members of the opposite sex cause pupil dilation and members of the opposite sex with dilated pupils are rated as more attractive than those with smaller pupils (Hess, 1975). The stimuli do not even have to be real. For example, the pupil constricts more when seeing a picture of the sun compared to viewing an indoor scene of equal brightness. Even imagining a bright stimulus leads to pupil constriction (Mathôt & Stigchel, 2015 for review). Pupil size is also influenced by cognitive tasks, such as mental arithmetic and number recall (Beatty, 1982; Granholm et al., 1996; Steinhauer et al., 2004; Laeng et al., 2012).

The pupils of non-human animals are also subject to influences other than light. For example, several authors (Beer, 1897; Magnus, 1902; Weel & Thore, 1936) have noted that when groups of cephalopods were kept within the same tank, and therefore exposed to very similar light levels, their pupils were constricted to varying degrees. It is therefore not surprising that extensive pupil movements are often seen in cephalopods despite the lack of any change in light level (Douglas et al., 2005). For example, their pupils dilate when they are ‘aroused’ during fighting, mating or viewing food (Beer, 1897; Bateson, 1890; Weel & Thore, 1936; Packard & Sanders, 1971; Muntz, 1977; Hurley et al., 1978). A large pupil, even in bright light, might serve a number of functions. It could, for example, be an intraspecific signal during courtship displays (Wells, 1966; Packard, 1972) or be part of a series of deimatic displays that help create the illusion of larger size when facing a potential predator (Wells, 1966; Hanlon & Messenger, 1988, 1996; Messenger, 2001). Because small pupils increase depth of field, a large pupil may also facilitate depth perception if the accommodative system is being monitored to provide information about object distance (Section 8.3.1).

Another group of animals whose pupil size seems only loosely related to changes in ambient illumination are birds. While pupil area often changes relatively little despite quite large variation in ambient illumination (Section 3.2.2), pupillary diameter can change markedly even without any obvious alteration in light level. The wide variation in pupil diameter under seemingly constant light conditions prompted several earlier authors to suggest the bird pupil might be subject to voluntary control (Harris, 1904; Mann, 1931; Walls, 1942).

More specific visual stimuli can sometimes have a greater effect on pupil diameter in birds than simple changes in illumination. For example, the chicken pupil constricts more to isoluminant red stimuli than it does to a change in overall light flux (Barbur et al., 2002; Moayed et al., 2012; Fig. 8). This suggests that the colour red may have a special significance to the animal. Various behavioural studies, for example, show that chickens prefer the colour red in a variety of situations (Roper & Marples, 1997; Salzen et al., 1971; Ham & Osorio, 2007).

The pupils of birds also respond to non-visual stimuli, dilating, for example, to sound (Loewenfeld, 1958; Bala & Takahashi, 2000). Pupils of a 'talking' parrot also constricted bilaterally prior to, and during, vocalisation, and when "attending" to the speech of others (Gregory & Hopkins, 1974). Whether such constriction serves a useful function, such as a social signal "commanding other birds attention" (Gregory & Hopkins, 1974) or is simply an expression of arousal is unclear. Sound also leads to pupil dilation in other vertebrates, such as cats (Watanabe et al., 1990).

Non-light related pupil activity has also been reported in reptiles. The pupils of snakes dilate when the animal is "excited, angry or frightened" (Munro, 1949), but constrict in response to tactile stimuli (Fontenot, 2008). It has also been suggested that in geckos, a dilated pupil is a sign of aggression, and that constriction of the pupil might serve to inhibit aggression from other individuals (Werner, 1972). Thus, some reptiles, like birds, may have a degree of voluntary control over pupil diameter (Denton, 1956; Werner, 1972). Given the striated nature of the iris muscles in these species (Section 2), this cannot be completely discounted. The neural substrates for such voluntary control are, however, unknown.

8.3 The iris and pupil in accommodation

8.3.1 The pupil near response

In humans and other higher primates, the pupil constricts on viewing close objects, which, due to the consequent increase in depth of field, along with the accompanying accommodative lens changes and ocular convergence (the near triad), serves to improve image quality (McDougal & Gamlin, 2015).

Some reptiles (Ott et al., 1998; Henze et al., 2004) and birds (Schaeffel et al., 1986; Schaeffel & Wagner, 1992; Glasser et al., 1997) also show pupillary constriction on accommodation. However, in birds at least, the extent of this near response, and its binocular nature, depends on the species. Accommodation is always accompanied by a near pupillary constriction in barn owls and, like accommodation in this species, is symmetrical in the two eyes (Schaeffel & Wagner, 1992). However, in the chicken, whose eyes are more laterally positioned, constriction of the pupil is not as strongly correlated with accommodative effort, especially in younger chickens, and the responses are independent in the two eyes (Schaeffel et al., 1986).

In primates, all three components of the near triad are independent, in the sense that one does not cause the other two. They simply have a common cause. However, in reptiles and birds the iris muscles are actively involved in changing the focus of the lens by ‘squeezing’ it (Ott, 2006), so that changes in pupil area when viewing close objects may simply be a by-product of accommodation.

There is also one situation in which a small pupil when viewing close objects is a disadvantage. Many animals with laterally placed eyes use monocular cues, such as the accommodative state of their eye, to determine their separation from an object (Collett & Harkness, 1982). However, eyes with a single small aperture have a large depth of field, minimising the need for accommodation. Consequently, animals with a single constricted pupillary aperture cannot use the accommodative state of the eye as a cue to distance. This may explain why cephalopods, a group of animals that are able to judge distances with accuracy (Wells, 1966; Chung & Marshall, 2014), maintain a wide pupil when viewing close objects such as prey (Weel & Thore, 1936; Wells, 1966), making accommodation a more useful cue to distance. Similarly, it has been suggested that chameleons, who are known to monitor their accommodation to judge distance, maintain wide pupils when aiming their tongues at prey even in high light levels (Harkness, 1977), although the existence of a pupil near response in these animals (Ott et al., 1998) is hard to reconcile with such a suggestion. The possession of multiple constricted pupillary apertures overcomes the problems caused by the greater depth of field of single stenopaic openings (Section 9.3)

8.3.2 A role for the pupil in amphibious vision

The curvature of the cornea, and its higher refractive index than air, ensure it is the major refractive surface in non-aquatic animals. Underwater, however, the cornea loses its refractive ability, as its front and rear surfaces border aqueous media of similar refractive index. The lenses of aquatic species are therefore the major refractive element, and consequently are spherical, and optically more powerful, than the relatively flattened lenses of terrestrial species.

This presents amphibious animals, which would benefit from seeing in both media, with an obvious problem. If they have the optics of a typical terrestrial animal, when their eyes are submerged, they will become hyperopic, as the cornea is lost as a refractive surface. Conversely, animals with the rounded lenses typical of aquatic animals will be very myopic in air. Conventional methods of accommodation could not provide focussed vision in both media. Nonetheless, by both refractive and behavioural measures, many amphibious mammals, birds and snakes have been shown to have similar visual abilities in air and water (Schusterman & Balliet, 1971; Herman et al., 1975; Howland & Sivak, 1984; Sivak et al., 1987, 1989; Ballard et al., 1989; Murphy et al., 1990; Schaeffel & Mathis, 1991; Katzir & Howland, 2003).

One way of achieving this is to have a powerful lens suitable for underwater vision, while minimizing the refractive capability of the cornea in air, by either reducing its overall curvature or incorporating flattened facets (Wilson, 1970; Howland & Sivak, 1984; Dawson et al., 1987; Sivak et al., 1987, 1989; Hanke et al., 2006, 2009). In addition, many aquatic mammals, for example, have spherical lenses typical of aquatic animals (West et al., 1991), but constrict their pupil to form a single stenopaic aperture in air, thereby affording a large depth of field (Sivak et al., 1989; Levenson & Schusterman, 1997; Hanke et al., 2006, 2009).

Pupillary constriction to increase depth of field may also explain the counterintuitive constriction of the pupil in aquatic snakes when submerged, and the lack of a relationship between the level of illumination and pupil size (Schaeffel & de Queiroz, 1990; Fontenot, 2008; Section 3.3.2). Constricting the pupil underwater, despite the fact that light levels are lower here than on land, would serve to maintain spatial acuity. Interestingly, humans may be able to do something analogous. The Moken, are a nomadic tribe of sea gypsies whose children forage underwater, often without facemasks. Their acuity underwater is about twice as good as that of untrained Europeans, a feat they achieve by maximal accommodation and constricting their pupils (Gislen et al., 2003, 2006).

An alternative method of ensuring adequate vision in both air and water is to have a pliable flattened lens in air, which is forced through a rigid pupil formed by well-developed iris musculature when underwater. This forms a highly refractive curved ‘nipple’ on the anterior surface of the lens, allowing some amphibious species to accommodate by as much as 50-60D (Sivak, 1980; Levy & Sivak, 1980; Murphy et al., 1990; Katzir & Howland, 2003).

9. The significance of pupil shape

While most dilated pupils are close to circular, on constriction they can take on a variety of forms; some remain circular, while others become elliptical or form narrow vertical or horizontal slits. Some, constricted pupils take on even more complex shapes, including; crescent moons, Ws, and multiple pinholes. The distribution of pupil shapes has been noted in section 3 and here their functional significance will be discussed.

9.1 Dorsal operculae

In several vertebrates, the dorsal iris protrudes into the pupil forming an operculum or umbraculum (umbrella). In most instances, the area of the pupil covered by the operculum increases as light levels rise. Such structures are relatively rare in terrestrial animals, but have been described in the rock hyrax (Millar, 1973). Several amphibia also have projections from the dorsal edge of the pupil (Section 3.4.2.1) and the corpora nigra extending from the dorsal iris of ungulates is functionally equivalent (Section 3.1.1; Fig. 4D). However, operculae are most well developed in animals living underwater, such as; cetaceans (Section 3.1.1; Fig. 4C), bottom dwelling skates and rays (Section 3.5.1; Figs. 14A&B), as well as substrate-living teleosts (Section 3.5.1; Figs. 13F, 14C&D). The W-shaped pupil of *Sepia* (Section 3.6.1; Fig. 18E), and the crescent-shaped aperture of some squid (Fig. 18C), are also formed by operculae.

Such dorsal intrusions could have several functions. Perhaps most obviously, in animals that live on the substrate, operculae would help disguise the very visible dark, circular, pupil, especially when seen from above (Section 7.2). Furthermore, the light field, especially underwater, is very uneven. Dorsal operculae will reduce the intensity of the potentially dazzling, or even damaging, downwelling light, while leaving the dimmer illumination from other directions less attenuated (e.g. Mäthger et al., 2013; Section 9.4).

Another advantage of a fully constricted opercular pupil is that, like a slit pupil (Section 9.2.1), it can potentially close down to much greater degree than a circular one, virtually preventing the access of any illumination. Operculae can also have irregular serrated edges (Figs. 14B-D), so that when constricted these overlap the ventral iris forming multiple small apertures (Franz, 1931; Murphy & Howland, 1991; Sivak & Luer, 1991; Gruber & Cohen, 1978) the function of which will be discussed in section 9.3.

9.1.1 Crescent-shaped pupils

Dorsal iris operculae can result in U-shaped or crescent-like pupils in some cetaceans (Section 3.1.1), substrate-dwelling fish (Section 3.5.1; Figs. 13F, 14), and cephalopods (Section 3.6.1; Fig. 18C). As noted above, such pupils may camouflage the eye when seen from above and selectively reduce the amount of downwelling illumination. They also enlarge the visual field slightly in comparison to a circular pupil, enhance the contrast of high spatial frequencies, could be used as a focus indicator (Section 9.4), and reduce the effect of diffraction while limiting the depth of field (Murphy & Howland, 1991).

In a lens with a uniform refractive index, such as a glass marble, light rays passing through the lens periphery are focussed closer to the lens than more central rays (Fig. 25), resulting in large amounts of positive spherical aberration and reduced image quality. The lenses of most animals suffer from far less spherical aberration than a marble, as they have refractive index gradients, with outer shells having a reduced refractive index compared to more central ones. In terrestrial animals, the effects of spherical aberration within the lens are further minimised as the cornea is the major refractive surface and the pupil can constrict, limiting the passage of light to only part of the lens. However, underwater the cornea is lost as a refractive element (Section 8.3.2), so that the lens is the only refractive surface. Furthermore, in most teleost fish, the lens protrudes through an immobile pupil, so that the whole lens is involved in image formation.

Although, fish lenses are generally well corrected for spherical aberration (Sivak, 1990 for review; Jagger, 1992; Kröger & Campbell, 1996; Kröger et al, 1994, 2001; Garner et al., 2001; Schartau et al., 2009), it has been suggested that a constricted crescent-shaped pupil could fulfil a similar function to the mobile circular pupil of other animals (section 7.1), reducing spherical aberration by restricting light to only part of the lens (Murphy & Howland, 1991). It could be argued that, if crescent-shaped pupils in fish serve to decrease spherical aberration, the lenses of species with such pupils would show greater degrees of spherical aberration than those of species with large, immobile, circular, pupils.

In comparison to a marble, both suckermouth catfish, who have crescent-shaped pupils, and goldfish, whose pupils are immobile, circular, and large, have significantly less spherical aberration. However, the lenses of both species are equally well corrected, each lens showing only small differences in back vertex distance for laser beams passing through the lens at different pupil heights, with both animals displaying a balance between negative 3rd order and a positive 5th order aberrations (Fig. 25). As the catfish lens is not perfectly corrected for spherical aberration, restricting light to the lens periphery through a crescent-shaped pupil will lead to a small, but significant, improvement of image quality. However, goldfish, arguably a more visual species than the catfish, have a similar degree of aberration yet, since they have large immobile pupils, must use the whole of their lens to form an image.

This might suggest that it is unlikely that the main purpose of the crescent-shaped pupil in suckermouth catfish is to decrease the effects of spherical aberration. This is in line with the observation that the clearnose skate, which also has a crescent-shaped pupil, similarly displays very little spherical aberration (Sivak, 1991; Sivak & Luer, 1991). However, it is important to note that the absence of a crescent-shaped pupil in goldfish does not necessarily mean it cannot reduce aberration in catfish. Evolution does not universally impose the same solution to a specific problem on all animals.

9.2 Elongated pupils

Substantially elongated pupils are rare in teleost fish and occur in only one species of bird (Zusi & Bridge, 1981). However, in mammals (Section 3.1.1), reptiles (Section 3.3.1), amphibia (Section 3.4.2.1), and elasmobranchs (Section 3.5.1) both horizontally and vertically elongated pupils are widespread. There is broad agreement that in terrestrial animals, based largely on work on snakes, but encompassing other groups too, that vertically elongated pupils are found in largely nocturnal or polyphasic ambush predators. Diurnal active predators have circular pupils and horizontally elongate pupils are common in herbivorous prey species (Walls, 1942; Mann, 1931; Brischoux et al., 2010; Banks et al., 2015).

Theoretically, there are a number of functional advantages elongated pupils have over circular ones, which need not always be mutually exclusive. Three of these are discussed further below. Additionally, elongated pupils may play a role in camouflaging the eye, which is discussed further elsewhere (Section 7.2).

9.2.1 Allow a greater range of aperture sizes

In a recent survey of pupil shapes in terrestrial animals (Banks et al., 2015), pupils were classified as either; circular, subcircular, vertical slits or horizontal. The horizontally elongated pupils, such as found in many ungulates (Section 3.1.1; Fig. 4D), were not considered true slits due to their rectangular shape. However, the elongated pupils of many elasmobranchs (Section 3.5.1) probably can be considered slits, whatever their orientation.

Constriction of a circular pupil by a sphincter muscle running around the pupillary margin (Fig. 2A) can normally only change retinal illuminance to a limited degree, as there are physical spatial constraints limiting the size of the constricted aperture (Walls, 1942). For example, the circular pupils of humans (Section 3.1.2.3.1) and dogs (Section 3.1.2.3.5) change in area by a factor of only about 16 and 2 respectively, and the reduction in retinal illumination this produces is relatively modest (1.2 & 0.3 log units, respectively). However, the lateral sphincter muscles in the irises of animals with slit-like pupils are composed of two bundles crossing above and below the pupil and contract with a “scissor-like” action (Raselli, 1923; Fig. 2B), allowing a much greater reduction in pupil area. Thus, the large dilated circular pupils of the cat and elephant seal, for example, form narrow vertical slits on constriction, decreasing pupil area by a factor of 135 and 469 respectively (Section 3.1.2.3.5), allowing greater attenuation of retinal illumination (2.1 & 2.7 log units).

An animal whose eye is adapted for vision in low light levels by, for example, the possession of a tapetum lucidum and a retina dominated by sensitive rods, may be compromised in daylight if it relied on a circular pupil. Slit-like pupils among terrestrial species are therefore usually found in predominantly nocturnal animals that nevertheless are sometimes abroad during the day (Walls, 1942; Mann, 1931; Brischoux et al., 2010; Rival et al., 2015; Banks et al., 2015). Strictly diurnal or nocturnal terrestrial animals, on the other hand, tend to have circular pupils, as they would derive less benefit from being able to adapt to a wide range of illumination. Among elasmobranchs, however, the situation is less clear; although slit pupils are common among nocturnal species and circular pupils are found in diurnal animals, there are a number of exceptions (Section 3.5.1).

Although this is the traditional explanation for the presence of a slit pupil, as pointed out by Land (2006), the suggestion that slit pupils necessarily allow greater pupillary closure than circular ones is “not entirely convincing”. Some animals with circular pupils, such as tarsiers, are able to form very small pinholes when constricted (Walls, 1942; Duke-Elder, 1958). Similarly, the circular pupil of hamsters can become very constricted following pharmacological manipulation (Hut et al., 2008), even though such constriction might never be reached in natural conditions. Thus, some animals with circular pupils can constrict their pupil to a great extent, suggesting slit pupils might have other functions, at least in some animals.

9.2.2 Decrease the effect of chromatic aberration

Image quality is degraded by longitudinal chromatic aberration, which occurs because the refractive index of a substance varies with wavelength. Short wavelengths are refracted more strongly than longer ones and are therefore focused closer to a lens, causing image blur if a range of wavelengths form the image.

Some animals minimise the chromatic blur circle by using multifocal lenses (Kröger et al., 1999), which consist of concentric shells of differing refractive index, each shell focussing a specific wavelength on the retina (Fig. 26A). Thus, there is one plane in the retina in which several wavelengths are sharply focussed. The efficacy of such multifocal lenses is reduced by a constricted circular pupil as it will shade the outer shells of the lens (Fig. 26B), so that some wavelengths will not be focussed on the retina (Malmström & Kröger, 2006). As elongated pupils allow the entire width of the lens to be involved in image formation, even in high light levels, they could be an adaptation for reducing the effects of chromatic aberration (Fig. 26C).

However, some animals, such as many birds and mice, have multifocal lenses yet pupils that are circular when constricted (Malmström & Kröger, 2006; Lind et al., 2008). This requires explanation, as it does not fit easily with the preceding argument. The solution proposed (Lind et al., 2008) is a ‘switching pupil’, in which the transition from fully dilated to constricted pupils occurs over a narrow range of light intensities. The dilated pupil will benefit from the multifocal optics of the lens, while the fully constricted pupil may have little need for them due to its large depth of field. The potentially detrimental effects of intermediate states of pupil constriction are minimised by the rapid ‘switching’ between constricted and dilated states.

9.2.3 Enhance vision for certain orientations

Neither of the above arguments explains why some pupils are elongated in the vertical direction and others in the horizontal (Banks et al., 2015). Specifically, why do terrestrial nocturnal ambush predators tend to have vertically elongated pupils, while in herbivores they are horizontally elongated? It may be related to their different foraging modes.

It was suggested that vertically elongated pupils will increase the depth of field in the horizontal plane (Heath et al., 1969; Brischoux et al., 2010) and that this might explain the presence of such pupils in nocturnal sit-and-wait foraging snakes, whose prey will approach in the horizontal plane relative to the head of the predator (Brischoux et al., 2010). However, Banks et al. (2015) have argued that with a vertically elongated pupil, the depth of field will in fact be greater for vertical contours, so that a range of distances will be in focus, whereas images of horizontal contours at different distances will be blurred. Ambush predators must be able to estimate distances accurately to catch their prey. The increased vertical depth of field will allow them to use stereopsis to estimate distances of vertical contours, while defocus blur can be used to judge distances of horizontal objects.

Herbivorous animals, likely to be preyed upon by others, must be able to detect potential predators approaching along the ground to avoid capture. This is aided by the horizontally elongated pupils of these species as, in contrast to vertical pupils, they reduce image blur in the horizontal plane, improving the image quality of objects on the ground (Banks et al., 2015). A horizontally elongated pupil also allows the eye to capture more light in the important horizontal plane, while reducing the amount of light from less important directions.

If elongated pupils indeed serve to improve object detection in various orientations, it is important that their orientation relative to the environment is maintained as the animal moves in space (Land, 2015). Appropriate compensatory eye movements have been observed in several herbivorous mammals (Banks et al., 2015), and some reptiles (Section 3.3.1), as well as in cephalopods (Section 3.6.1).

9.3 Multiple apertures

The constricted pupil in several species forms two or more apertures. The most obvious example are several species of gecko, where the constricted pupil forms four vertically aligned pinholes (Fig. 9C). Similarly, the dorsal operculae of some fish have serrated edges (Fig. 14), so that when these overlap the ventral iris margin several pinholes arranged into a crescent can be formed. Less spectacularly, the elongated constricted pupils of many sharks have a small aperture at either end of the slit (Fig. 13B), and the pupil of one of the few teleost fish to undergo pupillary closure, the plainfin midshipman, also consists of two small apertures (Fig. 13D). Similar pupils are found in some cetaceans (Section 3.1.1; Fig. 4C), as well as in a few terrestrial vertebrates (Murphy & Howland, 1991 for review) including horses (Miller & Murphy, 2016; Fig. 4E). The pupil of some cephalopods, such as cuttlefish (Muntz, 1977) and octopus (Fig. 18B), can also constrict to form two apertures.

Multiple pinholes, like other constricted pupil shapes, will decrease retinal illumination, but will result in slightly larger visual fields than a single aperture with a similar area (Walls, 1942). Furthermore, as long as the apertures are equidistant from the optical axis, such pupils, like the crescent-shaped pupils discussed above (Section 9.1.1) and small single aperture pupils (Section 7.1), will decrease the effects of spherical aberration (Murphy & Howland, 1991; Miller & Murphy, 2016). However, the big advantage multiple aperture pupils have over those with a single small aperture is their effect on depth of field. As noted previously (Section 8.3.1), many animals, especially those with lateral eyes, judge the distance of objects, by monitoring their accommodative system (Collett & Harkness, 1982). A single small aperture has a large depth of field making accommodation a less reliable measure of distance. This is probably why cephalopods (Section 8.2) and chameleons (Section 8.3.1) have large pupils when viewing nearby prey. Multiple pinholes would serve a similar purpose as, like larger pupils, they have a reduced depth of field; only images in the focal plane forming a single image on the retina, all other distances giving multiple images (Denton, 1956; Murphy & Howland, 1986, 1991; Banks et al., 2015). An animal with multiple pupillary apertures must accommodate precisely to obtain a focussed image and thus has a very accurate measure of distance even when its pupil is constricted.

9.4 The W-shaped pupil of the cuttlefish

The constricted pupil of cuttlefish often approximates the shape of a W (Section 3.6.1; Fig. 18E). Like other irregular pupil shapes, this could serve a cryptic function (Section 7.2; Douglas et al., 2005). In a similar way to that suggested for crescent-shaped pupils (Section 9.1.1), the constricted pupil of cuttlefish could also indicate the sign of defocus which could be used to guide accommodation (Schaeffel et al., 1999): The pupil would be imaged as an upright or an inverted W, depending on where the object is focused relative to the retina. However, neither of these explanations fully accounts for the shape of the cuttlefish pupil. Camouflage is, for example, an unlikely function when the cuttlefish is away from the ocean floor. Furthermore, its pupil will only appear as a W when seen from the side. From in front and behind, both of which are behaviourally important to cuttlefish, the pupil will be a vertical slit, negating its effectiveness as a focus indicator (Mäthger et al., 2013).

An alternative explanation for the shape of the cuttlefish pupil has therefore been proposed (Mäthger et al., 2013). By comparing the distribution of the underwater light field and the shape of the pupil when viewed from different directions, it seems that the most likely function of the constricted cuttlefish pupil is to balance the vertically uneven light field. It will reduce light from the dorsal part of the visual field more than horizontal illumination, thus minimising scattering of direct sunlight, improving the contrast of objects in dimmer parts of the visual scene.

Cephalopods often exhibit spectacular changes in colour, both for camouflage and display (Messenger, 2001; Mäthger et al., 2009). It has therefore always been rather disappointing that an animal with otherwise such a sophisticated visual system seems to be colour blind. ERG recordings, visual pigment extraction, and behavioural spectral sensitivity measures, all indicate most cephalopods have only a single visual pigment (Wells, 1978; Hanlon & Messenger, 1996; Muntz, 1999 for reviews). They also cannot be trained to distinguish colours (Messenger et al., 1973; Messenger, 1977), and only match their body pigmentation to the background intensity rather than wavelength (Marshall & Messenger, 1996; Mäthger et al, 2006). Thus, with the exception of the firefly squid (Michinomae et al., 1994), the weight of evidence is against colour vision in cephalopods. However, it has recently been suggested that the peculiar shape of the *Sepia* pupil might, in theory, allow the animal to perceive colour through exploiting spherical aberration in a non-axial pupil (Stubbs & Stubbs, 2016a&b). However, the utility of such a mechanism in the natural environment has been questioned (Gagnon et al., 2016), and it will need extensive behavioural verification in order to counteract the weight of evidence indicating the lack of chromatic discrimination by cephalopods.

9.5 Aphakic spaces

In most animals, the iris completely covers the periphery of the lens. However, in three genera of diurnal arboreal colubrid snake the pupil is elongated and often described as ‘keyhole-shaped’. As the pupil is horizontally wider than the lens, the rostral portion of the pupil is not filled by the lens (Mann, 1931; Walls, 1942; Henderson & Binder, 1980). Apart from these few snakes, such aphakic gaps have only been reported in fish. Although they occur in some elasmobranchs (Franz, 1931), they are most frequent in teleosts and can be of two basic forms (Munk & Frederiksen, 1974): Usually, only a portion of the pupil, often located rostrally, is unfilled by the lens, resulting in a tear-drop shaped pupil (Fig. 27). In some bathypelagic species, however, the aphakic space can be circumlental; with a spherical lens surrounded by a larger circular pupil.

Lateral-eyed animals, such as most snakes and fish, will normally have a restricted frontal field of view. Whilst a large lateral monocular field of view is clearly important to such animals, behaviourally relevant stimuli also occur in front of the animal, especially if they are moving in that direction. Rostral aphakic spaces, which are often associated with ‘sighting’ grooves on the head, will significantly increase the frontal binocular visual field (Walls, 1942; Henderson & Binder, 1980; Warrant & Locket, 2004). Light from objects in front of the animals will reach the lens through the rostral aphakic space and be imaged on the temporal retina which usually contains a region of high photoreceptor density (Section 9.6), allowing detailed analysis of objects in front of the animal and facilitating accurate binocular estimation of their distance.

During accommodation, rather than changing the curvature of their lens, fish move their lens towards and away from the retina (Sivak, 1980; Ott, 2006). As the lens protrudes through the pupil, such movements would only be possible in a plane perpendicular to the pupil if the lens completely filled a circular pupil. Aphakic gaps allow lens movements in the plane of the pupil. Rostral aphakic gaps would facilitate accommodative lens movements along a rostral-caudal axis, further enhancing frontal vision (Sivak, 1978, 1979).

Circumlental aphakic spaces, which occur primarily in fish inhabiting the light-restricted bathypelagic zone, apart from increasing the visual field in all directions, may aid sensitivity by increasing retinal illumination (Munk & Frederiksen, 1974; Warrant & Locket, 2004).

9.6 Retinal topography and pupil shape

The structure of the retina is rarely, if ever, uniform across its entire surface. Different areas are specialised for specific functions: Areas of increased cone and ganglion cell density, for example, are associated with higher resolution due to finer sampling of the visual field and less convergence of photoreceptor output. However, even if it were desirable to have the entire retina composed of tightly packed cones linked to individual ganglion cells to maximise visual acuity throughout the visual field, this would not be energetically sustainable and would require an unreasonably large optic nerve and excessive central processing. Thus, such retinal specializations only cover some of the retina and subtend just a small part of the visual field. As it is reasonable to expect such regions to be positioned so as to sample visual space mostly appropriately for any given species, they, not surprisingly, take on a variety of forms and are found in different locations within the retinae of various species, which can be related to the life style of the animal (Hughes, 1977; Collin, 1999; Moore et al., 2016).

Single areas of increased photoreceptor/ganglion cell density, such as the human fovea, are common. Horizontal visual streaks of increased cell density aligned with the horizon are also widespread in vertebrates (Hughes, 1977; Collin & Pettigrew, 1988b; Collin, 1999; Lisney & Collin, 2008; Moore et al., 2016) as well as cephalopods (Muntz, 1999; Talbot & Marshall, 2010, 2011). Thus, terrestrial vertebrates grazing in the open plains or aquatic organisms foraging near the substrate will benefit from sampling the horizon most thoroughly in order to keep a lookout for potential predators and detecting prey.

Two or more separate areas of increased cell density are also frequently observed. Bottom dwelling armoured catfish, for example, have two areas of high ganglion cell density; one located in the temporal retina, affording high resolution of objects in front of the animal, and a second area in the nasal retina facilitating increased resolution of objects from behind (Douglas et al., 2002). A similar arrangement is observed in, for example, other teleost fish (Collin & Pettigrew, 1988a; Collin, 1988) and cetacea (Mass & Supin, 2007).

Sometimes the shape and location of these specialised retinal areas appears to be mirrored by the form of the constricted pupil. Many ungulates, for example, have horizontally elongated pupils (section 3.1.1) and frequently have retinal streaks with a similar orientation (Schiviz et al., 2008; Moore et al., 2016). A similar correlation exists in some cephalopods (Talbot & Marshall, 2011). Notable is the pyjama squid, which lies buried in the substrate with only the tops of its laterally positioned eyes protruding. As a pupil located centrally would be looking at the mud, the pupil of this species is shifted dorsally, while the ventral retina has a band of high photoreceptor density (Talbot & Marshall, 2010). Similarly, other aquatic animals with a nasal and temporal area of high ganglion cell density sometimes have either crescent shaped pupils (Douglas et al., 2002), tapered pupils (Collin & Pettigrew, 1988a) or, as in cetaceans (section 3.1.1), pupils consisting of two small pinholes.

However, pupillary shape and the form of any retinal specialisation are frequently not in synchrony. Many mammals, such as rabbits (Hughes, 1977) and several species of Artiodactyla (Schiviz et al., 2008), for example, have elongated visual streaks yet posses circular pupils. Similalrly, teleost fishes (Collin & Pettigrew, 1988a&b; Collin, 1999) and birds have a plethora of forms of retinal specialisations, yet virtually all have simple circular pupils (sections 3.2.1 and 3.5.2.3). Similarly, elasmobranchs with horizontal visual streaks can have either horizontal or vertical slit pupils (McComb et al., 2009) and cats have vertical slit pupils (Fig. 4B) yet have a horizontal retinal streak (Hughes, 1977).. These are just a few of the many examples suggesting pupil shape and the form of any retinal specialisation are usually not coincident.

In fact, it would in some ways be surprising to find any similarities between the locations of retinal specialisations and pupil shape. In humans, the pupil is located at the nodal point of the eye. Consequently, the pupil functions as an aperture stop, affecting the amount of light reaching the retina. It is not a field stop. Perceptually, this is obvious as our field of view does not shrink as the pupil constricts. Thus, if a horizontally elongated pupil of an ungulate, for example, aligned with the horizon also acts as an aperture stop, it will not affect the visual field. It will, however, maximise the amount of illumination reaching the eye from the possibly more relevant lateral directions, while decreasing the amount of 'distracting' vertical illumination.

In the horse, however, the pupil is located in front of the nodal point of the eye. As a result, in this species the horizontal rectangular shape of the pupil will give it a wider view of the horizon than would a circular pupil of the same surface area (Murphy & Howland, 1986; Miller & Murphy, 2016). This affords the horse an extended view of the horizon, while reducing the variation in brightness between the sky and ground.

10. Conclusions

Apart from teleost fish, the majority of vertebrates and cephalopods have pupils whose area decreases as light levels rise. However, the degree of constriction is highly variable, ranging from relatively modest in, for example, most birds and amphibia, to changes in area of over 100 fold in some Carnivora. In general, animals active in low light levels, who may nonetheless sometimes be abroad during the day, and thus are exposed to a large range of light levels, have the greatest range of pupil sizes.

The rate of pupillary constriction is also very variable. Constriction can occur in little more than a second in cephalopods and birds, but take many minutes in, for example, nocturnal sharks. The fast pupil response of birds is a result of their striated iris musculature, and may be an adaptation to the rapid changes in light level sometimes experienced during flight. However, for animals that only use their pupil to adapt to the more gradual changes in light level experienced at twilight, a much slower rate of change is appropriate.

In birds and sharks, diurnal species have a higher threshold for pupil constriction than nocturnal animals, presumably because their retinae are less sensitive. It is likely the same holds true for other animals.

Pupil responses are uncommon in teleost fish, and largely restricted to bottom-dwelling species, suggesting a role in camouflaging the eye, rather than vision. However, it remains unclear why all teleosts do not make use of the other, visual, advantages offered by a mobile pupil.

Representatives of all vertebrate groups and cephalopods, contrary to earlier assumptions, have varying degrees of consensual pupil responses. In general, animals with lateral eyes tend to have a lesser consensual response than species whose eyes are forward facing. Consensuality may aid binocular fusion, facilitating stereoscopic depth perception in animals with frontally positioned eyes. Lateral-eyed animals, on the other hand, will benefit from the two eyes behaving independently, as they will view quite different visual scenes and may perform unrelated tasks.

Perhaps the most surprising development in visual science in the last 20 years has been the identification of a class of novel, non-rod non-cone, photoreceptor in the retina. These newly described photoreceptors are involved in various non-image forming functions of the eye, which require the assessment of overall light levels, rather than detailed image formation. Not surprisingly, these melanopsin-containing, intrinsically-photosensitive retinal ganglion cells are also involved in the PLR of many, and perhaps most, vertebrates. Although their precise role in regulating pupil size remains to be fully defined, they are principally involved in sustained responses at high light levels.

The autonomic control of iris muscles is relatively conserved across different vertebrates, although the nature of the receptor on the effector muscle is variable. In mammals, birds, and reptiles, parasympathetic innervation activates the sphincter muscle and sympathetic fibres usually control the dilator. The picture for amphibia is less clear, perhaps due to the predominance of direct sphincter photosensitivity and the possible absence of dilator muscles. In both teleost and elasmobranch fish, the roles of the sympathetic and parasympathetic pathways are reversed compared to other vertebrates; the parasympathetic system activating the dilator and sympathetic fibres controlling the sphincter muscle, although it is still uncertain whether the elasmobranch sphincter muscle receives any direct innervation at all.

Many animals show a degree of light-evoked pupil constriction even in the absence of retinal input. Such intrinsic iris photosensitivity is especially well-developed in amphibia, but occurs in all groups of vertebrate and cephalopods. It is, however, not universal. An opsin-based visual pigment, such as rhodopsin or melanopsin, located in the sarcolemma of the sphincter muscle is coupled, via a G-protein, to a smooth muscle contraction cascade involving phospholipase C. Such intrinsic iris responses allow sustained pupillary constriction, even when retinal illumination is reduced by the pupil.

Functionally, changes in pupil area help balance the conflicting demands of retinal sensitivity and spatial acuity; dilation serving to enhance retinal illumination in low light levels, and constriction resulting in improved image quality in brighter light by decreasing the amount of spherical aberration imposed by the lens. In some species, most notably substrate-dwelling teleost fish and some reptiles, pupil constriction serves mainly to camouflage the eye by obscuring the otherwise very conspicuous pupil.

As the changes in light level experienced by most animals far exceed the variation in retinal illumination produced by changes in pupil area, pupillary changes are not sufficient to adjust fully the sensitivity of the retina during light and dark adaptation. They are, perhaps, a rapid mechanism that can smooth out the effects of fast changes in light levels until other, more efficient, ways of adjusting retinal sensitivity take over.

It is well known that in humans, the pupil is subject to small rhythmic changes in size in constant illumination (hippus), and endogenous circadian clocks influence pupil size. The same is true for the pupils of several other species. Similarly, in humans stimulus colour can influence pupil size, even in the absence of changes in total light flux. Chickens also respond most vigorously to equiluminant red stimuli. Psychological factors such as cognitive load and arousal also affect human pupil size. The pupils of non-human animals are also subject to such ‘internal’ stimuli that are unrelated to light. In ‘aroused’ cephalopods, for example, pupillary area may be important in courtship and deimatic displays. Tactile and auditory stimuli also affect pupil size. Although members of all vertebrate and cephalopods groups display pupil responses unrelated to ambient illumination, this property is particularly apparent in birds and cephalopods. It is furthermore possible, that the striated iris muscles of reptiles and birds are subject to a degree of voluntary control.

The pupils of some animals, like those of humans, constrict when viewing close objects. However, since constricted pupils have a larger depth of field, some animals with lateral eyes maintain a dilated pupil at near, to enable the use of accommodation as an accurate cue to object distance. The greater depth of field afforded by a constricted pupil is also used by some amphibious species to compensate for the lack of a refractive cornea underwater, allowing focussed vision in both air and water.

While dilated pupils in most species are circular, constricted pupil shape is highly variable, and, depending on species, can be; circular, elliptical/rectangular, a narrow vertical or horizontal slit, or have a more complex shape, such as a crescent, or even consist of multiple apertures.

- Dorsal operculae are common, especially in aquatic species, and potentially serve a number of functions, including; compensating for the uneven light field underwater, disguising the eye when seen from above, and reducing the degree of spherical aberration.

- Elongated pupils could also serve a number of functions, for example; allowing a large range of pupil areas in animals active in widely varying conditions of illumination, permitting the whole lens to be used to allow multifocal lenses to offset the effects of chromatic aberration, and enhancing object detection in specific orientations.
- The main advantage of pupils consisting of multiple apertures may be that, unlike constricted single apertures, they have a narrow depth of field, allowing accommodation to be used as an accurate indicator of object distance.
- The remarkable W-shaped pupils of cuttlefish most likely serve to balance the unevenly distributed underwater light field. Although it has recently been suggested they could, theoretically, facilitate colour vision in animals such as cuttlefish with only a single visual pigment, the weight of evidence indicates cuttlefish cannot perceive colour.
- Rostral aphakic gaps, often resulting in 'tear drop' shaped pupils in some fish and snakes, will increase the frontal visual field in such lateral-eyed animals, and allow fish to accommodate in the plane of the pupil, further enhancing frontal vision.
- Although most animals have variously shaped areas of retinal specialisation, such as regions of increased photoreceptor or ganglion cell density, as the pupil acts as an aperture stop rather than a field stop, the form of these areas is largely independent of the shape of the pupil.

Although convincing arguments can be made to explain the shape of the pupils of many animals, a multitude of questions remain unanswered: Why, for example, are almost all bird pupils circular, and why do some frogs have vertical slit pupils while in others they are horizontal, even when the animals seem to occupy similar optical environments?

11. Acknowledgements and disclosures

I am grateful to Jochen Wagner, Julian Partridge, and Liz White for permission to use unpublished data and to Justin Marshall for providing many of the photographs. Other pictures were provided by Ray Caldwell, Andre Rivamonte, Steve Parish, and Sarah Douglas. Thanks also to Chris Murphy, Paul Gamlin, Jon Erichsen, Ronald Kröger, Almut Kelber, Olle Lind, David Gower, Jim Dearworth, Tony Redmond, Shaun Collin, Mike Land and Barbara Wueringer, who answered many questions, made suggestions or provided access to original data and figures. Especial gratitude to Chris Hull and John Barbur for their innumerable explanations of what I know were very basic concepts and to Mike Powner for help with figures.

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

References

Alexandridis, E., 1967a. Pupillographische Untersuchung der Netzhautempfindlichkeit des Taubenauges. Graefes Arch. Clin. Exp. Ophthalmol. 172(2), 139-151.

Alexandridis, E., 1967b. Oscillations in the pigeon's pupil servomechanism in relation to illumination. Cell. Mol. Life Sci. 23(2), 154-155.

Ali, M.A., 1975. Retinomotor responses, in: Ali, M.A. (Ed.), Vision in Fishes. Plenum Press, New York, pp. 313-355.

Allcock, A.L., Lindgren, A., Strugnell, J.M., 2015. The contribution of molecular data to our understanding of cephalopod evolution and systematics: a review. J. Nat. Hist. 49(21-24), 1373-1421.

Allen, E.R., Neill, W.T., 1950. The vertical position of the pupil in crocodilians and snakes. Herpetologica 6(3), 95-96.

Amat, F., Wollenberg, K.C., Vences, M., 2013. Correlates of eye colour and pattern in mantellid frogs. Salamandra 49(1), 7-17.

Armstrong, P.B., Bell, A.L., 1968. Pupillary responses in the toad as related to innervation of the iris. Am. J. Physiol. 214(3), 566-573.

Arrese, C., Archer, M., Runham, P., Dunlop, S. A., Beazley, L. D., 2000. Visual system in a diurnal marsupial, the numbat (*Myrmecobius fasciatus*): retinal organization, visual acuity and visual fields. Brain Behav. Evolut. 55(4), 163-175.

Arrese, C., 2002. Pupillary mobility in four species of marsupials with differing lifestyles. J. Zool. 256(2), 191-197.

Bailes, H.J., Trezise, A.E.O., Collin, S.P., 2007. The optics of the growing lungfish eye: Lens shape, focal ratio and pupillary movements in *Neoceratodus forsteri* (Krefft, 1870). Visual Neurosci. 24(3), 377-387.

Bailes, H. J., Lucas, R. J., 2010. Melanopsin and inner retinal photoreception. Cell. Mol. Life Sci. 67, 99-111.

Bala, A.D.S., Takahashi, T.T., 2000. Pupillary dilation response as an indicator of auditory discrimination in the barn owl. J. Comp. Physiol. A 186(5), 425-434.

Ballard, K. A., Sivak, J. G., Howland, H. C., 1989. Intraocular muscles of the Canadian river otter and Canadian beaver and their optical function. Can. J. Zool. 67, 469-474.

Banks, M.S., Sprague, W.W., Schmoll, J., Parnell, J.A., Love, G.D., 2015. Why do animal eyes have pupils of different shapes?. Sci. Adv. 1(7), p.e1500391.

Barbur, J. L., Forsyth, P. M., 1986. Can the pupil response be used as a measure of the visual input associated with the geniculo-striate pathway? Clin. Vision Sci. 1, 107–111.

Barbur, J. L., Harlow, A. J., Sahraie, A., 1992. Pupillary responses to stimulus structure, colour and movement. Ophthal. Physiol. Opt. 12, 137–141.

Barbur, J.L., Prescott, N.B., Douglas, R.H., Jarvis, J.R., Wathes, C.M., 2002. A comparative study of stimulus-specific pupil responses in the domestic fowl (*Gallus gallus domesticus*) and the human. Vision Res. 42(2), 249-55.

Barbur, J.L. (2004). Learning from the pupil - studies of basic mechanisms and clinical applications, in: Chalupa, L.M., Werner, J.S. (Eds.), The Visual Neurosciences, volume 1. MIT Press, Cambridge, pp. 641-656.

Barr, L., Alpern, M., 1963. Photosensitivity of the frog iris. J. Gen. Physiol. 46, 1249-1265.

Barr, L., Gu, F.J., 1986. Photomechanical coupling in the frog iris has no threshold and is not mediated by a membrane potential change or by extracellular calcium entry. Biophys. J. 49(2), A285-A285.

Barr, L., Gu, F.J., 1987. A quantitative model of myosin phosphorylation and the photomechanical response of the isolated sphincter pupillae of the frog iris. Biophys. J. 51(6), 895-904.

Barr, L., 1988. Hypersensitivity to light of the iris (Sphincter pupillae) of the albino axolotl (*Ambystoma mexicanum*). J. Exp. Biol. 137, 589-596.

Barr, L., 1989. Photomechanical coupling in the vertebrate sphincter pupillae. Crit. Rev. Neurobiol. 4(4), 325-366.

Barrio-Asensio, C., Murillo-González, J., Peña-Meliánn, A., Puerta-Fonollá, J., 1999. Immunocytochemical study on the triple origin of the sphincter iris in the chick embryo. Dev. Genes Evol. 209(10), 620-624.

Barsotti, G., Briganti, A., Spratte, J.R., Ceccherelli, R., Breghi, G., 2010a. Bilateral mydriasis in common buzzards (*Buteo buteo*) and little owls (*Athene noctua*) induced by concurrent topical administration of rocuronium bromide. Vet. Ophthalmol. 13(s1), 35-40.

Barsotti, G., Briganti, A., Spratte, J.R., Ceccherelli, R., Breghi, G., 2010b. Mydriatic effect of topically applied rocuronium bromide in tawny owls (*Strix aluco*): comparison between two protocols. Vet. Ophthalmol. 13(s1), 9-13.

Barsotti, G., Briganti, A., Spratte, J.R., Ceccherelli, R., Breghi, G., 2012. Safety and efficacy of bilateral topical application of rocuronium bromide for mydriasis in European kestrels (*Falco tinnunculus*). J. Avian Med. Surg. *26*(1), 1-5.

Bateson, W., 1890. Contractility of the iris in fishes and cephalopods. J. Mar. Biol. Assoc. U.K. 1, 215-216.

Baver, S.B., Pickard, G.E., Sollars, P.J., 2008. Two types of melanopsin retinal ganglion cell differentially innervate the hypothalamic suprachiasmatic nucleus and the olivary pretectal nucleus. Eur. J. Neurosci. 27, 1763–1770.

Beatty, J., 1982. Task-evoked pupillary responses, processing load, and the structure of processing resources. Psychol. Bull. 91, 276–292.

Beer, T., 1894. Die Accommodation des Fischauges. Pflügers Arch. Ges. Physiol. 58, 523-650.

Beer, T., 1897. Die Accommodation des Cephalopodenauges. Pflügers Arch. Ges. Physiol. 67, 541-586.

Bell, A.L., 1965. The fine structure of the iris of the eel. J. Cell Biol. 27, 9A-10A.

Beltran, W.A., Vanore, M., Ollivet, F., Nemoz-Bertholet, F., Aujard, F., Clerc, B., Chahory, S., 2007. Ocular findings in two colonies of gray mouse lemurs (*Microcebus murinus*). Vet. Ophthalmol. 10(1), 43-49.

Berlucchi, G., Strata, P., 1964. The problem of a true consensual light reflex in birds. Arch. Ital. Biol. 102(1), 29-35.

Berson, D.M., Dunn, F.A., Takao, M., 2002. Phototransduction by retinal ganglion cells that set the circadian clock. Science 295, 1070–1073.

Bisazza, A., Rogers, L.J., Vallortigara, G., 1998. The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. Neurosci. Biobehav. R. 22(3), 411-426.

Bishop, L. G., Stark, L., 1965. Pupillary responses in the screech owl, *Otus asio*. Science 148, 1750–1752

Bishop, P.O., Pettigrew, J.D., 1986. Neural mechanisms of binocular vision. Vision Res. 26, 1587–600.

Bito, L.Z., Turansky, D.G., 1975. Photoactivation of pupillary constriction in the isolated in vitro iris of a mammal (*Mesocricetus auratus*). Comp. Biochem. Phys. A 50(2), 407-413.

Bjerager, P., Heegaard, S., Taugaard, J., 2003. Anatomy of the eye of the sperm whale (*Physeter macrocephalus L*.). Aquat. Mamm. 29(1), 31–36.

Blaustein, D.I., Dewey, M.M., 1979. Localization of rhodopsin in osmotically intact rod outer segment discs. J. Histochem. Cytochem. 27(3), 788-793.

Bonmati-Carrion, M.A., Hild, K., Isherwood, C., Sweeney, S.J., Revell, V.L., Skene, D.J., Rol, M.A., Madrid, J.A., 2016. Relationship between human pupillary light reflex and circadian system status. PloS One 11(9), p.e0162476.

Bozzano, A., Pankhurst, P.M., Moltschaniwskyj, N.A., Villanueva, R., 2009. Eye development in southern calamary, *Sepioteuthis australis*, embryos and hatchlings. Mar. Biol. 156, 1359–1373.

Bradley, M.M., Miccoli, L., Escrig, M.A., Lang, P.J., 2008. The pupil as a measure of emotional arousal and autonomic activation. Psychophysiology 45, 602–607.

Brischoux, F., Pizzatto, L., Shine, R., 2010. Insights into the adaptive significance of vertical pupil shape in snakes. J. Evolution. Biol. 23(9), 1878-1885.

Bron A.J., Tripathi, R.C., Tripathi, B.J., 1997. Wolff's Anatomy of the Eye and Orbit, eigth ed. Chapman & Hall, London.

Brown-Séquard, E., 1847a. Recherches exprimentales sur l'action de la lumiere et sur celle d'un changement de temperature sur l'iris, dans les cinq classes d'animaux vertebres. C. R. Acad. Sci. Paris 25, 482-483.

Brown-Séquard, E., 1847b. Note complementaire d'un memoire sur l'action de la lumire et d'un changement de temperature sur l'iris. C. R. Acad. Sci. Paris 25, 508-510.

Brown-Séquard, E., 1859. Recherches experimentales sur l'influence de la lumiere, du froid et de la chaleur sur l'iris dans les cinq classe d'animaux vertebres. J. Physiol. Homme Anim. 2, 281-294.

Brudenall, D.K., Schwab, I.R., Fritsches, K.A., 2008. Ocular morphology of the Leatherback sea turtle (*Dermochelys coriacea*). Vet. Ophthalmol. 11(2), 99-110.

Budelmann, B.U., Young, J.Z., 1984. The statocyst-oculomotor system of *Octopus vulgaris*: extraocular eye muscles, eye muscle nerves, statocyst nerves and the oculomotor centre in the central nervous system. Philos. T. Roy. Soc. B 306(1127), 159-189.

Burnside, B., Nagle, B., 1983. Retinomotor movements of photoreceptors and retinal pigment epithelium: mechanisms and regulation. Prog. Retin. Res. 2, 67-109.

Burnside, B., Kingsmith, C., 2010. Fish retinomotor movements, in: Dartt, D.A., Besharse, J., Danz, R. (Eds.), Encyclopaedia of the Eye. Academic Press, Oxford, pp. 142-150.

Byrne, R. A., Kuba, M., Griebel, U., 2002. Lateral asymmetry of eye use in *Octopus vulgaris.* Anim. Behav. 64, 461-468.

Calcagnini, G., Giovannelli, P., Censi, F., Bartolini, P. and Barbaro, V., 2001. Baroreceptor-sensitive fluctuations of heart rate and pupil diameter. In Engineering in Medicine and Biology Society, 2001. Proceedings of the 23rd Annual International Conference of the IEEE (Vol. 1, pp. 600-603). IEEE.

Campbell, H.S., Smith, J.L., 1962. The pharmacology of the pigeon pupil. Arch. Ophthalmol. 67, 501–505.

Campenhausen, C. von, 1963. Quantitative Beziehungen zwischen Lichtreiz und Kontraktion des Musculus sphincter pupillae vom Scheibenzüngler (*Discoglossus pictus*). Biol. Cybern. 1(6), 249-267.

Carpenter, M. B., Pierson, R. J., 1973. Pretectal region and the pupillary light reflex. An anatomical analysis in the monkey. J. Comp. Neurol. 149, 271–300.

Chichery, R., Chanelet, J., 1972. Effect of acetylcholine and various curarizing substances on the nervous system of sepia. C. R. Seances Soc. Biol. Fil. 166(2), 273-276.

Cheng, S., Dearworth, J.R., Esckilsen, S.J., Kubera, C.L., Anderson, C.R., Goldberg, L.A., Selvarajah, B.P., D'souza, M.S., Hartnett, L.P., Chejlava, M.J., Sherma, J., Perlow, D.R., Ho, E., 2017. Melanopsin mRNA in the iris of red-eared slider turtles (*Trachemys scripta elegans). J. Herpetol.* 51(4), 538-551.

Chung, W.-S., Marshall, N.J., 2014. Range-finding in squid using retinal deformation and image blur. Curr. Biol. 24(2), R64-R65.

Chung, W.-S., Marshall, N.J., 2017. Complex visual adaptation in squid for specific tasks in different environments. Front. Physiol. 8, article 105.

Clarke, R.J., Zhang, H., Gamlin, P.D., 2003. Characteristics of the pupillary light reflex in the alert rhesus monkey. J. Neurophysiol. 89(6), 3179-3189.

Collett, T.S., Harkness, L.I.K., 1982. Depth vision in animals, in: Ingle, D.J., Goodale, M.A., Mansfield, R.J.W. (Eds.), Analysis of Visual Behaviour. MIT Press, Cambridge, pp. 111-176.

Collin, S. P., 1988. The retina of the shovel-nosed ray, *Rhinobatos batillum* (Rhinobatidae): morphology and quantitative analysis of the ganglion, amacrine and bipolar cell populations. Exp. Biol. 47, 195-207.

Collin, S. P., Pettigrew, J. D., 1988a. Retinal topography in reef teleosts. I. Some species with well-developed areae but poorly-developed streaks. Brain Behav. Evolut. 31, 269-282.

Collin, S. P., Pettigrew, J. D., 1988b. Retinal topography in reef teleosts. II. Some species with prominent horizontal streaks and high density areae. Brain Behav. Evolut. 31, 283-295.

Collin, S.P., 1999. Behavioural ecology and retinal cell topography, in: Archer, S.N., Djamgoz, M.B.A., Loew, E.R., Partridge, J.C., Vallerga, S. (Eds.), Adaptive Mechanisms in the Ecology of Vision. Kluwer Academic Publishers, Dordrecht, pp. 509-535.

Cornell, E.A., Hailman, J.P., 1984. Pupillary responses of two *Rana pipiens*-complex anuran species. Herpetologica 40(4), 356-366.

Cott, H.B., 1940. Adaptive Coloration in Animals. Methuen & Co, London.

Courjon, D., 1977. Considerations on visual acuity of reptiles as a function of pupil diaphragmation. Opt. Acta 24(8), 897-906.

Davidson, G.L., Butler, S., Fernández-Juricic, E., Thornton, A., Clayton, N.S., 2014. Gaze sensitivity: function and mechanisms from sensory and cognitive perspectives. Anim. Behav. 87, 3-15.

Davies, W.I., Tamai, T.K., Zheng, L., Fu, J.K., Rihel, J., Foster, R.G., Whitmore, D., Hankins, M.W., 2015. An extended family of novel vertebrate photopigments is widely expressed and displays a diversity of function. Genome Res. 25(11), 1666-1679.

Davis, J.L., Stewart, T., Brazik, E., Gilger, B.C., 2003. The effect of topical administration of atropine sulfate on the normal equine pupil: influence of age, breed and gender. Vet. Ophthalmol. 6(4), 329-332.

Dawson, W.W., Adams, C.K., Barris, M.C., Litzkow, C.A., 1979. Static and kinetic properties of the dolphin pupil. Am. J. Physiol.-Reg. I. 237(5), R301-R305.

Dawson, W. W., Schroeder, J. P., Sharpe, S. N., 1987. Corneal surface properties of two marine mammal species. Mar. Mammal Sci. 3(2), 186–197.

Dearworth, J.R., Cooper, L.J., McGee, C., 2007. Parasympathetic control of the pupillary light response in the red-eared slider turtle (*Pseudemys scripta elegans*). Vet. Ophthalmol. 10(2), 106-110.

Dearworth, J.R., Cooper, L.J., 2008. Sympathetic influence on the pupillary light response in the red-eared slider turtle (*Pseudemys scripta elegans*). Vet. Opthalmol. 11(6), 306-313.

Dearworth, J.R., Brenner, J.E., Blaum, J.F., Littlefield, T.E., Fink, D.A., Romano, J.M., Jones, M.S., 2009. Pupil constriction evoked in vitro by stimulation of the oculomotor nerve in the turtle (*Trachemys scripta elegans*). Visual Neurosci. 26(3), 309-318.

Dearworth, J.R., Sipe, G.O., Cooper, L.J., Brune, E.E., Boyd, A.L., Riegel, R.A.L., 2010. Consensual pupillary light response in the red-eared slider turtle (*Pseudemys scripta elegans*). Vision Res. 50(6), 598-605.

Dearworth, J.R., Selvarajah, B.P., Kalman, R.A., Lanzone, A.J., Goch, A.M., Boyd, A.B., Goldberg, L.A., Cooper, L.J., 2011. A mammalian melanopsin in the retina of a fresh water turtle, the red-eared slider (*Trachemys scripta elegans*). Vision Res. 51(2), 288-295.

Denton, E.J., 1956. The response of the pupil of *Gekko gecko* to external light stimulus. J. Gen. Physiol. 40(2), 201-216.

Denton, E. J., 1990. Light and vision at depths greater than 200 metres, in: Herring, P.J., Campbell, A.K., Whitfield, M., Maddocks, L. (Eds.), Light and Life in the Sea. Cambridge University Press, Cambridge, pp. 127-148.

Dieterich, H.J., Fischer, G., Hiller, U., 1988. The smooth muscle of the iris of the Gray Parrot (*Psittacus erithacus*). Z. mikrosk. anat. Forsc. 102, 239-250.

Douglas, R.H., Harper, R.D., Case, J.F., 1998. The pupil response of a teleost fish, *Porichthys notatus*: description and comparison to other species. Vision Res. 38, 2697-2710.

Douglas, R.H., Collin, S.P., Corrigan, J., 2002. The eyes of suckermouth armoured catfish (Loricariidae, subfamilty Hypostomus): pupil response, lenticular longitudinal spherical aberration and retinal topography. J. Exp. Biol. 205, 3425-3433.

Douglas, R.H., Williamson, R., Wagner H.-J., 2005. The pupillary response of cephalopods. J. Exp. Biol. 208, 261-265.

Drager, U.C., 1978. Observations on monocular deprivation in mice. J. Neurophysiol. 41, 28–42.

Duke-Elder, S., 1958. System of Ophthalmology. Vol 1. The Eye in Evolution. Henry Kimpton, London.

Ducret, S., Kogo, S., 1931. Untersuchungen über den Einfluss der Sympathicusreizung auf die Retina. Pflügers Arch. Ges. Physiol. 227, 71-80.

Ebbesson, S.O.E., 1984. Evolution and ontogeny of neural circuits. Brain Behav. Sci. 7, 321-366

Ecker, J.L., Dumitrescu, O.N., Wong, K.Y., Alam, N.M., Chen, S.-K., LeGates, T., Renna, J.M., Prusky, G.T., Berson, D.M., Hattar, S., 2010. Melanopsin-expressing retinal ganglion-cell photoreceptors: Cellular diversity and role in pattern vision. Neuron 67, 49–60.

Fontenot, C.L., 2008. Variation in pupil diameter in North American Gartersnakes (*Thamnophis*) is regulated by immersion in water, not by light intensity. Vision Res. 48(15), 1663-1669.

Foster, R. G., Hankins, M. W., 2002. Non-rod, non-cone photoreception in the vertebrates. Prog. Retin. Eye Res. 21, 507-527.

Frankenberg, E., 1979. Pupillary response to light in Gekkonid lizards having various times of daily activity. Vision Res. 19(3), 235-245.

Franz, V., 1905. Zur Anatomie, Histologie und functionellen Gestaltung des Selachierauges. Jenaische Zeitschrift für Naturwissenschaft 40, 697-840.

Franz, V., 1906. Beobachtungen am lebenden Selachierauge. Jenaische Zeitschrift für Naturwissenschaft 41, 429-471.

Franz, V., 1931. Die Akkommodation des Selachierauges und seine Abblendungsapparate, nebst Befunden an der Retina. Zool. Jahrb. Allg. Zool. 49, 325-462.

Freedman, M.S., Lucas, R.J., Soni, B., von Schantz, M., Munoz, M., David-Gray, Z., Foster, R.G., 1999. Regulation of mammalian circadian behavior by non-rod, non-cone, ocular photoreceptors. Science 284, 502–504.

Froesch, D., 1973. On the fine structure of the Octopus iris. Cell Tissue Res. 145(1), 119-129.

Fujimoto, M., Kunioka, H., Katayama, H., 1995. Pharmacology of the retractor lentis muscle of the bluegill (*Lepomis macrochirus*). J. Comp. Physiol. A 176, 673-677.

Gabella, G., Clarke, E., 1983. Embryonic development of the smooth and striated musculatures of the chicken iris. Cell Tissue Res. 229(1), 37-59.

Gagnon, Y.L., Osorio, D.C., Wardillc, T.J., Marshall, N.J., Chung, W.-S., Temple, S.E., 2016. Can chromatic aberration enable color vision in natural environments? Proc. Natl. Acad. Sci. U.S.A. 113(45), E6908-6909.

Gamlin, P.D., Reiner, A., Erichsen, J.T., Karten, H.J., Cohen, D.H., 1984. The neural substrate for the pupillary light reflex in the pigeon (*Columba livia*). J. Comp. Neurol. 226(4), 523-543.

Gamlin, P.D.R., Zhang, H., Harlow, A., Barbur, J.L., 1998. Pupil responses to stimulus color, structure and light flux increments in the rhesus monkey. Vision Res. 38, 3353–3358.

Gamlin, P.D., McDougal, D.H., Pokorny, J., Smith, V.C., Yau, K.W., Dacey, D.M., 2007. Human and macaque pupil responses driven by melanopsin-containing retinal ganglion cells. Vision Res. 47, 946–954.

Garner, L. F., Smith, G., Yao, S., Augusteyn, R. C., 2001. Gradient refractive index of the crystalline lens of the black oreo dory (*Allocyttus niger*): comparison of magnetic resonance imaging (MRI) and laser raytrace methods. Vision Res. 41, 973-979.

Ghosh, S., Salvador-Silva, M., Coca-Prados, M., 2004. The bovine iris-ciliary epithelium expresses components of rod phototransduction. Neurosci. Lett. 370, 7–12.

Gilbert, P.W., Sivak, J.G., Pelham, R.E., 1981. Rapid pupil change in selachians. Can. J. Zool. 59(3), 560-564.

Gislen, A., Dacke, M., Kröger, R.H.H., Abrahamsson, M., Nilsson, D.E., Warrant, E.J., 2003. Superior underwater vision in a human population of sea gypsies. Curr. Biol. 13, 33–836.

Gislen, A., Warrant, E.J., Dacke, M., Kröger, R.H.H., 2006. Visual training improves underwater vision in children. Vision Res. 48, 3443–3450.

Glasser, A., Pardue, M.T., Andison, M.E., Sivak, J.G., 1997. A behavioural study of refraction, corneal curvature, and accommodation in raptor eyes. Can. J. Zool. 75, 2010–2020.

Glaus-Most, L., 1969. Zur Lichtreaktion der isolierten Froschiris. Rev. Suisse Zool. 76(43), 799-848.

Glaw, F., Vences, M., 1997. Anuran eye colouration: definitions, variation, taxonomic implications and possible functions. Herpetologia Bonnensis. SEH Proceedings, Bonn, 125-138.

Granda, A.M., Dearworth, J.R., Kittila, C.A., Boyd, W.D., 1995. The pupillary response to light in the turtle. Visual Neurosci. 12, 1127-1133.

Granholm, E., Asarnow, R.F., Sarkin, A.J., Dykes, K.L., 1996. Pupillary responses index cognitive resource limitations. Psychophysiology 33, 457–461.

Gregory, R.L., Hopkins, S., 1974. Pupils of a talking parrot. Nature 252(5485), 637-638.

Grozdanic, S., Sakaguchi, D.S., Kwon, Y.H., Kardon, R.H., Sonea, I.M., 2002. Characterization of the pupil light reflex, electroretinogram and tonometric parameters in healthy rat eyes. Curr. Eye Res. 25(2), 69-78.

Grozdanic, S., Betts, D.M., Allbaugh, R.A., Sakaguchi, D.S., Kwon, Y.H., Kardon, R.H., Sonea, I.M., 2003. Characterization of the pupil light reflex, electroretinogram and tonometric parameters in healthy mouse eyes. Curr. Eye Res. 26(6), 371-378.

Grozdanic, S.D., Matic, M., Sakaguchi, D.S., Kardon, R.H., 2007. Evaluation of retinal status using chromatic pupil light reflex activity in healthy and diseased canine eyes. Invest. Ophth. Vis. Sci. 48(11), 5178-5183.

Gruber, S.H., 1967. A behavioural measurement of dark adaptation in the Lemon shark, *Negaprion brevirostris*, in: Gilbert, P.W., Mathewson, R.F., Rall, D.P. (Eds.), Sharks, Skates and Rays. John Hopkins Press, Baltimore, pp. 479-490.

Gruber, S. H., Cohen, J. L., 1978. Visual system of the elasmobranchs: state of the art 1960-1975, in: Hodgson, E.S., Mathewson, R.F. (Eds.), Sensory Biology of Sharks and Rays. Office of Naval Research, Arlington, pp. 11-105.

Grynfeltt, E., 1910. Les muscles de l'iris chez les téléostéens. Bibliographie Anatomique 20, 265-332.

Gundlach, R. H., 1934. The speed of pupillary contraction in response to light in pigeons, cats, and humans. J. Genet. Psychol. 44, 250–253.

Guth, E., 1901. Untersuchungen über die direkte motorische Wirkung des Lichtes auf den Sphincter Pupillae des Aal- und Frosch-auges. Pflügers Arch. Ges. Physiol. 85, 119-142.

Hafter, E., 1932. Untersuchungen über den Mechanismus der retinalen Umstimmung hinsichtlich einer Abhängigkeit vom vegetativen Nervensystem. Pflügers Arch. Ges. Physiol. 229(1), 447-465.

Ham, A.D., Osorio, D., 2007. Colour preferences and colour vision in poultry chicks. P. Roy. Soc. Lond. B Bio. 274, 1941–1948.

Hammond, P., Mouat, G.S.V., 1985. The relationship between feline pupil size and luminance. Exp. Brain Res. 59(3), 485-490.

Hanke, F.D., Dehnhardt, G., Schaeffel, F., Hanke, W., 2006. Corneal topography, refractive state, and accommodation in harbor seals (*Phoca vitulina*). Vision Res. 46, 837–847.

Hanke, F.D., Hanke, W., Scholtyssek, C., Dehnhardt, G., 2009. Basic mechanisms of pinniped vision. Exp. Brain Res. 199(3–4), 299–311.

Hanlon, R.T., Messenger, J.B., 1988. Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): the morphology and development of body patterns and their relation to behaviour. Philos. T. Roy. Soc. B 320(1200), 437-487.

Hanlon, R.T., Messenger, J.B., 1996. Cephalopod Behaviour. Cambridge University Press, Cambridge.

Harkness, L., 1977. Chameleons use accommodation cues to judge distance. Nature 267, 346-349.

Harris, W., 1904. Binocular and stereoscopic vision in man and other vertebrates, with its relation to the decussation of the optic nerves, the ocular movements, and the pupil light reflex. Brain 27, 103-174.

Hattar, S., Liao, H.W., Takao, M., Berson, D.M., Yau, K.W., 2002. Melanopsin-containing retinal ganglion cells: architecture, projections, and intrinsic photosensitivity. Science 295, 1065–1070.

Hattar, S., Lucas, R.J., Mrosovsky, N., Thompson, S., Douglas, R.H., Hankins, M.W., Lem, J., Biel, M., Hofmann, F., Foster, R.G., Yau, K.W., 2003. Melanopsin and rod–cone photoreceptive systems account for all major accessory visual functions in mice. Nature, 424(6944), 76-81.

Heath, J.E., Nothcutt, R.G., Barber, R.P., 1969. Rotational optokinesis in reptiles and its bearing on pupillary shape. Z. vergl. Physiol. 62, 75-85.

Heesy, C.P., 2004. On the relationship between orbit orientation and binocular visual field overlap in mammals. Anat. Rec. 281(1), 1104-1110.

Henderson, R.W., Binder, M.H., 1980. The ecology and behavior of vine snakes (*Ahaetulla*, *Oxybelis*, *Thelotornis*, *Uromacer*): a review. Mil. Pub. Mus. Cont. Biol. Geol. 37, 1–38.

Henning, J., Henning, P.A., Himstedt, W., 1991. Peripheral and central contribution to the pupillary reflex control in amphibians: pupillographic and theoretical considerations. Biol. Cybern. 64, 511-518.

Henning, J., Himstedt, W., 1994. The pathway controlling the pupillary light reflex in urodeles. Exp. Brain Res. 98(3), 412-420.

Henze, M.J., Schaeffel, F., Wagner, H.-J., Ott, M., 2004. Accommodation behaviour during prey capture in the Vietnamese leaf turtle (*Geoemyda spengleri*). J. Comp. Physiol. A 190(2), 139–146.

Herman, L.M., Peacock, M.F., Yunker, M.P., Madsen, C.J., 1975. Bottlenosed dolphin: double slit pupil yields equivalent aerial and underwater visual acuity. Science 189, 650–652.

Hess, E.H., 1975. The role of pupil size in communication. Sci. Am. 233(5), 110-119.

Himstedt, W., 1995. Structure and function of the eyes in the caecilian *Ichthyophis kohtaoensis* (Amphibia, Gymnophiona). Zoology (Jena) 99(1), 81-94.

Höfle, M., Kenntner-Mabiala, R., Pauli, P., Alpers, G.W., 2008. You can see pain in the eye: pupillometry as an index of pain intensity under different luminance conditions. Int. J. Psychophysiol. 70(3), 171-175.

Howland, H. C., Sivak, J. G., 1984. Penguin vision in air and water. Vision Res. 24, 1905-1909.

Hughes, A., 1977. The topography of vision in mammals of contrasting lifestyle: comparative optics and retinal organisation, in: Crescitelli, F. (Ed.), Handbook of Sensory Physiology, vol. 7/5. Springer, Berlin, pp. 613-756.

Hughes, A., 1979. A schematic eye for the rat. Vision Res. 19(5), 569-588.

Hughes, A., Vaney, D.I., 1982. The organization of binocular cortex in the primary visual area of the rabbit. J. Comp. Neurol. 204(2), 151-164.

Hurley, A. C., Lange, G. D., Hartline, P. H., 1978. The adjustable ‘pinhole’ eye of *Nautilus*. J. Exp. Zool. 205(1), 37-43.

Hussain, R.Z., Hopkins, S.C., Frohman, E.M., Eagar, T.N., Cravens, P.C., Greenberg, B.M., Vernino, S., Stüve, O., 2009. Direct and consensual murine pupillary reflex metrics: establishing normative values. Auton. Neurosci. 151(2), 164-167.

Hut, R.A., Oklejewicz, M., Rieux, C., Cooper, H.M., 2008. Photic sensitivity ranges of hamster pupillary and circadian phase responses do not overlap. J. Biol. Rhythm. 23(1), 37-48.

Inoue, T., 1980. Efferent discharge patterns in the ciliary nerve of rabbits and the pupillary light reflex. Brain Res. 186, 43-53.

Ishigaki, H., Miyao, M., Ishihara, S.Y., 1991. Change of pupil size as a function of exercise. J. Hum. Ergol. 20(1), 61-66.

Iske M.S., 1929. A study of the iris mechanism of the alligator. Anat. Rec. 44, 57–77.

Jagger, W. S., 1992. The optics of the spherical fish lens. Vision Res. 32, 1271-1284.

Jeffery, G., 2001. Architecture of the optic chiasm and the mechanisms that sculpt its development. Physiol. Rev. 81(4), 1393-1414.

Kallähn, S.V., 2014. Untersuchungen zur chromatischen Pupillometrie am Vogelauge (Doctoral dissertation, Ulm).

Kargacin, G.J., Detwiler, P.B., 1985. Light-evoked contraction of the photosensitive iris of the frog. J Neurosci. 5(11), 3081-3087.

Katzir, G., Howland, H. C., 2003. Corneal power and underwater accommodation in great cormorants (*Phalacrocorax carbo sinensis*). J. Exp. Biol. 206, 833–841.

Kim, J., Heo, J., Ji, D., Kim, M.S., 2015. Quantitative assessment of pupillary light reflex in normal and anesthetized dogs: a preliminary study. J. Vet. Med. Sci. 77(4), 475-478.

Kirby, M.L., Diab, I.M., Mattio, T.G., 1978. Development of adrenergic innervation of the iris and fluorescent ganglion cells in the choroid of the chick eye. Anat. Rec. 191(3), 311-319.

Kobayashi, H., Kohshima, S., 2001. Unique morphology of the human eye and its adaptive meaning: comparative studies on external morphology of the primate eye. J. Hum. Evol. 40(5), 419-435.

Kotsuka, K., Naito, H., 1960. The pupillodilating action of the oculomotor nerve of bull frogs: Efferent parasympathetic double innervation of the circular muscle of the iris. Med. J. Osaka Univ. 10, 397-411.

Kozicz, T., Bittencourt, J.C., May, P.J., Reiner, A., Gamlin, P.D.R., Palkovits, M., Horn, A.K.E., Toledo, C.A.B., Ryabinin, A.E., 2011. The Edinger-Westphal nucleus: A historical, structural and functional perspective on a dichotomous terminology. J. Comp. Neurol. 519(8), 1413–1434.

Krastel, H., Alexandridis E., 1972. Pupillenlichtreflexe beim grünen Leguan (*Iguana iguana*), in: Jaeger W. (Ed.), Cornea. Deutsche Ophthalmologische Gesellschaft (Bericht über die 71. Zusammenkunft in Heidelberg 1971), vol 71. J.F. Bergmann-Verlag, Munich, pp. 551-554.

Krivoshik, A.P., Barr, L., 2000. Force relaxes before the fall of cytosolic calcium in the photomechanical response of rat sphincter pupillae. Am. J. Physiol.-Cell Ph. 279(1), C274-C280.

Kröger, R.H.H., Kirschfeld, K., 1993. Optics of the harbor porpoise eye in water. J. Opt. Soc. Am. A 10(7), 1481-1489.

Kröger, R. H. H., Campbell, M. C. W., Munger, R., Fernald, R. D., 1994. Refractive index distribution and spherical aberration in the crystalline lens of the African cichlid fish, *Haplochromis burtoni.* Vision Res. 34, 1815-1822.

Kröger, R. H. H., Campbell, M. C. W., 1996. Dispersion and longitudinal chromatic aberration of the crystalline lens of the African cichlid fish *Haplochromis burtoni*. J. Opt. Soc. Am. A 13, 2341-2347.

Kröger, R. H. H., Campbell, M. C. W., Fernald, R. D., Wagner, H.-J., 1999. Multifocal lenses compensate for chromatic defocus in vertebrate eyes. J. Comp. Physiol. A 184, 361-369.

Kröger, R. H. H., Campbell, M. C. W., Fernald, R. D., 2001. The development of the crystalline lens is sensitive to visual input in the African cichlid fish, *Haplochromis burtoni.* Vision Res. 41, 549-559.

Kruger, D.J., Weldon, C., Minter, L.R., du Perez, L.H., 2013. Morphology of the elygium and developing umbraculum in the eye of *Amietia vertebralis* tadpoles. J. Morphol. 274(5), 551-556.

Kuchnow, K.P., Gilbert, P.W., 1967. Preliminary *in vivo* studies on pupillary and tapetal pigment responses in the lemon shark, *Negaprion brevirostris*, in: Gilbert, P.W., Mathewson, R.F., Rall, D.P. (Eds.), Sharks, Skates and Rays. John Hopkins Press, Baltimore, pp. 465-477.

Kuchnow, K.P., 1970. Threshold and action spectrum of the elasmobranch pupillary response. Vision Res. 10, 955-964.

Kuchnow, K.P., Martin, R., 1970. Fine structure of elasmobranch iris muscle. Exp. Eye Res. 10, 345-351.

Kuchnow, K.P., 1971. The elasmobranch pupillary response. Vision Res. 11, 1395-1406.

Kuchnow, K.P., Martin, R., 1972. Fine structure of the iris and associated structures of the skates *Raja asterias* and *R. clavata*. Exp. Eye Res. 13, 98-102.

Laeng, B., Sirois, S., Gredebäck, G., 2012. Pupillometry: A window to the preconscious? Perspect. Psychol. Sci. 7(1), 18–27.

Lall, G.S., Revell, V.L., Momiji, H., Enezi, J.A., Altimus, C.M., Güler A.D., Aguilar, C., Cameron, M.A., Allender, S., Hankins, M.W., Lucas, R.J., 2010. Distinct contributions of rod, cone, and melanopsin photoreceptors to encoding irradiance. Neuron 66, 417–428.

Lamb, T.D., Pugh, E.N., 2004. Dark adaptation and the retinoid cycle of vision. Prog. Retin. Eye Res. 23(3), 307-380.

Land, M.F., 2006. Visual optics: The shapes of pupil. Curr. Biol. 16(5), R167-R168.

Land, M.F., 2015. Eye movements of vertebrates and their relation to eye form and function. J. Comp. Physiol. A 201(2), 195-214.

Land, M.F., Nilsson, D.-E. 2012. Animal Eyes. Oxford University Press, Oxford.

Lanzing, W.J.R., Wright, R.G., 1981. The fine structure of the chromatophores and other non-sensory components of the eye of the blue-eye, *Pseudomugil signifer*. J. Fish Biol. 19(3), 269-284.

Lau, K.C., So, K.-F., Campbell, G., Lieberman, A.R., 1992. Pupillary constriction in response to light in rodents, which does not depend on central nervous pathways. J. Neurol. Sci. 113, 70-79.

Leff, A., 2004. A historical review of the representation of the visual field in primary visual cortex with special reference to the neural mechanisms underlying macular sparing. Brain Lang. 88(3), 268-278.

Levenson, D.H.,Schusterman, R.J., 1997. Pupillometry in seals and sea lions: ecological implications. Can. J. Zool. 75(12), 2050-2057.

Levenson, D.H., Schusterman, R.J., 1999. Dark adaptation and visual sensitivity in shallow and deep-diving pinnipeds. Mar. Mammal Sci. 15(4), 1303-1313.

Levine, J., 1955. Consensual pupillary response in birds. Science 122(3172), 690-690.

Levy, B., Sivak, J.G., 1980. Mechanisms of accommodation in the bird eye. J. Comp. Physiol. A 137, 267-272.

Li, T., Howland, H.C., 1999. A true neuronal consensual pupillary reflex in chicks. Vision Res. 39, 897–900.

Lind, O.E., Kelber, A., Kröger, R.H.H., 2008. Multifocal optical systems and pupil dynamics in birds. J. Exp. Biol. 211, 2752-2758.

Link, B. A., Nishi, E., 1998. Development of the avian iris and ciliary body: mechanisms of cellular differentiation during the smooth-to-striated muscle transition. Dev. Biol. 203, 163–176.

Lisney, T.J., Collin, S.P., 2008. Retinal ganglion cell distribution and retinal resolving power in elasmobranchs. Brain Behav. Evolut. 72, 59-77.

Loerzel, S.M., Smith, P.J., Howe, A., Samuelson, D.A., 2002. Vecuronium bromide, phenylephrine and atropine combinations as mydriatics in juvenile double-crested cormorants (*Phalacrocorax auritus*). Vet. Ophthalmol. 5(3), 149-154.

Loewenfeld, I.E., 1958. Mechanisms of reflex dilatation of the pupil. Doc. Ophthalmol. 12(1), 185-448.

Loewenfeld, I. E., 1993. The Pupil. Anatomy, Physiology, and Clinical Applications, Vol.1. Iowa State University Press, Ames, Wayne State University Press, Detroit.

Lowenstein, O., Friedman, E.D., 1942. Pupillographic studies. I. Present pupillography; its method and diagnostic significance. Arch. Ophthalmol. 27(5), 969–993.

Lowenstein, O., Murphy, S.B., Loewenfeld, I.E., 1953. Functional evaluation of the pupillary light reflex pathways: experimental pupillographic studies in cats. Arch. Ophthalmol. 49(6), 656-670.

Lowenstein, O., 1954. Clinical pupillary symptoms in lesions of the optic nerve, optic chiasm, and optic tract. Arch. Ophthalmol. 52, 385–403.

Lowenstein, O., Loewenfeld, I. E., 1959. The pupil, in: Davson, H. (Ed.), The Eye, Vol. 3, Muscular Mechanisms. Academic Press, New York, pp. 255-337.

Lucas, R.J., Freedman, M.S., Munoz, M., Garcia-Fernandez, J.M., Foster, R.G., 1999. Regulation of the mammalian pineal by non-rod, non-cone, ocular photoreceptors. Science 284, 505–507.

Lucas, R.J., Douglas, R.H., Foster, R.G., 2001. Characterization of an ocular photopigment capable of driving pupillary constriction in mice. Nat. Neurosci. 4(6), 621-626.

Lucas, R.J., Hattar, S., Takao, M., Berson, D.M., Foster, R.G., Yau, K.W., 2003. Diminished pupillary light reflex at high irradiances in melanopsin-knockout mice. Science 299, 245-247.

Lucas, R.J., 2013. Mammalian inner retinal photoreception . Curr. Biol. 23(3), R125-R133.

Lucas, R.J., Peirson, S.N., Berson, D.M., Brown, T.M., Cooper, H.M., Czeisler, C.A., Figueiro, M.G., Gamlin, P.D., Lockley, S.W., O'Hagan, J.B., Price, L.L.A., Provencio, I., Skene, D.J., Brainard, G.C., 2014. Measuring and using light in the melanopsin age. Trends Neurosci. 37, 1-9.

MacLaren, R.E., Pearson, R.A., MacNeil, A., Douglas, R.H., Salt, T.E., Akimoto, M., Swaroop, A., Sowden, J.C., Ali, R.R., 2006. Retinal repair by transplantation of photoreceptor precursors. Nature 444(7116), 203-207.

Magnus, R., 1899. Beiträge zur Pupillarreaction des Aal- und Froschauges. Ztschr. f. Biol. 20, 567-606.

Magnus, R., 1902. Die Pupillarreaction der Octopoden. Pflügers Arch. Ges. Physiol. 92, 623-643.

Malmström, T., Kröger, R.H.H., 2006. Pupil shapes and lens optics in the eyes of terrestrial vertebrates. J. Exp. Biol. 209, 18–25.

Mann, I., 1931. Iris patterns in the vertebrates. Trans. Zool. Soc. London 21, 355–412.

Markwell, E. L., Feigl, B., Zele, A. J., 2010. Intrinsically photosensitive melanopsin retinal ganglion cell contributions to the pupillary light reflex and circadian rhythm. Clin. Exp. Optom. 93, 137–149.

Marshall, N.J., Messenger, J.B., 1996. Colour-blind camouflage. Nature 382(6590), 408-409.

Martin, G.R., 1999. Eye structure and foraging in King Penguins *Aptenodytes patagonicus*. IBIS 141(3), 444-450.

Martin, G.R., 2007. Visual fields and their functions in birds. J. Ornithol. 148(suppl 2), S546–S562.

Martin, G.R., 2009. What is binocular vision for? A bird’s eye view. J. Vis. 9(11):14, 1–19.

Mass, A.M., 2001. Visual field organization and retinal resolution in the Beluga Whale *Delphinapterus leucas* (Pallas). Dokl. Biol. Sci. 381, 555–558.

Mass, A.M., Supin, A.Y., 2007. Adaptive features of aquatic mammals' eye. Anat. Rec. 290(6), 701-715.

Mäthger, L.M., Barbosa, A., Miner, S., Hanlon, R.T., 2006. Color blindness and contrast perception in cuttlefish (*Sepia officinalis*) determined by a visual sensorimotor assay. Vision Res. 46(11), 1746-1753.

Mäthger, L.M., Denton, E.J., Marshall, N.J., Hanlon, R.T., 2009. Mechanisms and behavioural functions of structural coloration in cephalopods. J. R. Soc Interface 6(Suppl 2), S149-S163.

Mäthger, L. M., Hanlon, R. T., Håkansson, J., Nilsson, D. E., 2013. The W-shaped pupil in cuttlefish (*Sepia officinalis*): functions for improving horizontal vision. Vision Res. 83, 19–24.

Mathôt, S., van der Stigchel, S., 2015. New light on the mind’s eye: The pupillary light response as active vision. Curr. Dir. Psychol. Sci. 24(5), 374-378.

Matsui, H., Takayama, G., Sakurai, Y., 2016. Physiological response of the eye to different colored light‑emitting diodes in Japanese flying squid *Todarodes pacificus*. Fisheries Sci. 82, 303–309.

McBrien, N.A., Moghaddam, H.O., New, R., Williams, L.R., 1993. Experimental myopia in a diurnal mammal (*Sciurus carolinensis*) with no accommodative ability. J. Physiol. 469(1), 427-441.

McComb, D.M., Tricas, T.C., Kajiura, S.M., 2009. Enhanced visual fields in hammerhead sharks. J. Exp. Biol. 212(24), 4010-4018.

McCormick, L.R., Cohen, J.H., 2012. Pupil light reflex in the Atlantic brief squid, *Lolliguncula brevis.* J. Exp. Biol. 215, 2677-2683.

McDougal, D. H., Gamlin, P. D., 2010. The influence of intrinsically photosensitive retinal ganglion cells on the spectral sensitivity and response dynamics of the human pupillary light reflex. Vision Res. 50, 72–87.

McDougal, D.H., Gamlin, P.D., 2015. Autonomic control of the eye. Compr. Physiol. 5, 439-473.

McGinley, M.J., Vinck, M., Reimer, J., Batista-Brito, R., Zagha, E., Cadwell, C.R., Tolias, A.S., Cardin, J.A., McCormick, D.A., 2015. Waking state: rapid variations modulate neural and behavioral responses. Neuron 87(6), 1143-1161.

Meekins, J.M., Stuckey, J.A., Carpenter, J.W., Armbrust, L., Higbie, C., Rankin, A.J., 2015. Ophthalmic diagnostic tests and ocular findings in a flock of captive American flamingos (*Phoenicopterus ruber ruber*). J. Avian Med. Surg. 29(2), 95-105.

Meredith, R.W., Janečka, J.E., Gatesy, J., Ryder, O.A., Fisher, C.A., Teeling, E.C., Goodbla, A., Eizirik, E., Simão, T.L., Stadler, T., Rabosky, D.L., 2011. Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. Science 334(6055), 521-524.

Messenger, J.B., Wilson, A.P., Hedge, A., 1973. Some evidence for colour-blindness in Octopus. J. Exp. Biol. 59(1), 77-94.

Messenger, J.B., 1977. Evidence that Octopus is colour blind. J. Exp. Biol. 70(1), 49-55.

Messenger, J.B., 2001. Cephalopod chromatophores: neurobiology and natural history. Biol. Rev. 76(4), 473-528.

Michinomae, M., Masuda, H., Seidou, M., Kito, Y., 1994. Structural basis for wavelength discrimination in the banked retina of the firefly squid *Watasenia scintillans*. J. Exp. Biol. 193(1), 1-12.

Mikaelian, I., Paillet, I., Williams, D., 1994. Comparative use of various mydriatic drugs in kestrels (*Falco tinnunculus*). Am. J. Vet. Res. 55, 270–272.

Millar RP. 1973. An unusual light-shielding structure in the eye of the dassie, *Procavia capensis* Pallas (Mammalia: Hyracoidea). Ann. Transvaal Mus. 28, 203–205.

Miller, P.E., Murphy, C.J., 2016. Equine vision, in: Gilger, B.C. (Ed.), Equine Ophthalmology 3rd edition. John Wiley & Sons Inc., Hoboken, pp. 508-544.

Miller, S.N., Colitz, C.M., Dubielzig, R.R., 2010. Anatomy of the California sea lion globe. Vet. Ophthalmol. 13(s1), 63-71.

Miller, S.N., Samuelson, D., Dubielzig, R., 2013. Anatomic features of the cetacean globe. Vet. Ophthalmol. 16(s1), 52-63.

Moayed, A.A., Choh, V., Hariri, S., Liu, C., Wong, A., Bizheva, K., 2012. Stimulus-specific pupil dynamics measured in birds (*Gallus gallus domesticus*) in vivo with ultrahigh resolution optical coherence tomography. Invest. Ophth. Vis. Sci. 53(11), 6863-6869.

Mohun, S.M., Davies, W.L., Bowmaker, J.K., Pisani, D., Himstedt, W., Gower, D.J., Hunt, D.M., Wilkinson, M., 2010. Identification and characterisation of visual pigments in caecilians (Amphibia: Gymnophiona), an order of limbless vertebrates with rudimentary eyes. J. Exp. Biol. 213(20), 3586-3592.

Mohun, S.M., Wilkinson, M., 2015. The eye of the caecilian *Rhinatrema bivittatum* (Amphibia: Gymnophiona: Rhinatrematidae). Acta Zool. 96(2), 147-153.

Moore, B.A., Tyrrell, L.P., Kamilar, J.M., Collin, S.P., Dominy, N.J., Hall, M.I., Heesy, C.P., Lisney, T.J., Loew, E.R., Moritz, G.L., Nava, S.S., Warrant, E., Yopak, K.E., Fernandez-Juricic, E., 2016. Structure and function of regional specializations in the vertebrate retina, in: Kaas, J (Ed.), Evolution of Nervous Systems 2e. vol. 1. Elsevier, Oxford, pp. 351–372.

Morris, J.L., 1976. Motor innervation of the toad iris *(Bufo marinus).* Am. J. Physiol. 231, 1272-1278.

Mughannam, A.J., Buyukmihci, N.C., Kass, P.H., 1999. Effect of topical atropine on intraocular pressure and pupil diameter in the normal horse eye. Vet. Ophthalmol. 2(4), 213-215.

Münch, M., Léon, L., Crippa, S.V., Kawasaki, A., 2012. Circadian and wake-dependent effects on the pupil light reflex in response to narrow-bandwidth light pulses. Invest. Ophth. Vis. Sci. 53(8), 4546-4555.

Munk, O., 1970. On the occurrence and significance of horizontal band-shaped retinal areae in teleosts. Vidensk. Medd. Dan. Naturhist. Foren. Khobenhavn 133, 85-120.

Munk, O., Frederiksen, R.D., 1974. On the function of aphakic apertures in teleosts. Vidensk. Meddr. Dansk. Naturh. Foren. 137, 65-94.

Munk, O., 1985. Intraocular smooth muscles of iris, anterior chamber angle, sclera, and choroid in the snake mackerel, *Gempylus serpens* Cuvier, 1829 (Pisces, teleostei). Vidensk. Meddr. Dansk. Naturh. Foren. 146, 21-45.

Munro, D.F., 1949. Vertical position of the pupil in the Crotalidae. Herpetologica 5(5), 106-108.

Munro, D.F. 1950. Vertical orientation of the eye in snakes. Herpetologica 6(3), 84-88.

Muntz, W.R.A., 1977. Pupillary response of cephalopods. Symp. Zool. Soc. Lond. 38, 277-285.

Muntz, W.R.A., 1999. Visual systems, behaviour, and environment in cephalopods. in: Archer, S.N., Djamgoz, M.B.A., Loew, E.R., Partridge, J.C., Vallerga, S. (Eds.), Adaptive Mechanisms in the Ecology of Vision. Kluwer Academic Publishers, Dordrecht, pp. 467-483.

Murphy, C.J., Howland, H.C., 1986. On the gekko pupil and Scheiner's disc. Vision Res. 26(5), 815-817.

Murphy, C.J., Bellhorn, R. W., Williams, T., Burns, M. S., Schaeffel, F., Howland, H. C., 1990. Refractive state, ocular anatomy, and accommodative range of the sea otter (*Enhydra lutris*). Vision Res. 30(1), 23–32.

Murphy, C.J., Howland, H.C., 1991. The functional significance of crescent-shaped pupils and multiple pupillary apertures. J. Exp. Zool. Suppl. 5, 22–28.

Nelson, J.S., 1994. Fishes of the World, third ed. John Wiley & Sons Inc. New York.

Nesis, K.N., 1987. Cephalopods of the World. T.F.H. Publications Inc. Neptune City.

Neudecker, S., 1989. Eye camouflage and false eyespots : chaetodontid responses to predators. Environ. Biol. Fish. 25(1-3), 143-157.

Neuhuber, W., Schrödl, F., 2011. Autonomic control of the eye and the iris. Auton. Neurosci. 165(1), 67-79.

New, S.T.D., Hemmi, J.M., Kerr, G.D., Bull, C.M., 2012. Ocular anatomy and retinal photoreceptors in a skink, the sleepy lizard (*Tiliqua rugosa*). Anat. Rec. 295, 1727-1735.

Nicol, J. A. C., 1978. Studies on the eye of the stingray *Dasyatis sabina*, with notes on other selachians. I. Eye dimensions, cornea, pupil and lens. Contrib. Mar. Sci. 21, 89-102.

Nilsson, S., 1980. Sympathetic nervous control of the iris sphincter of the Atlantic cod, *Gadus morhua.* J. Comp. Physiol. A 138, 149-155.

Nilsson, S., 1994. The iris, in: Nilsson, S., Holmgren, S. (Eds.), Comparative Physiology and Evolution of the Autonomic Nervous System. Harwood Academic Publishers, Chur, pp. 353–361.

Nishida, S., Sears, M., 1970. Fine structure of the anterior epithelial cell layer of the iris of the hen. Exp. Eye Res. 9, 241–245.

Nolte, J., Pointner, F., 1975. The fine structure of the iris of the grass frog, *Rana pipiens*. Cell Tissue Res. 158(1), 111-120.

Nunnally, J.C., Knott, P.D., Duchnowski, A., Parker, R., 1967. Pupillary response as a general measure of activation. Atten. Percept. Psychophys. 2(4), 149-155.

Nyitrai, G., Bardos, I., Veress, G., Gáspárdy, A., 2010. Evaluation of the neurological system's responsivity through the pupil of the racing pigeon. Magy. Állatorvosok 132(8), 479-488.

Oehme, H. van, 1969. Der Bewegungsapparat der Vogeliris (eine vergleichende morphologisch-funktionelle Untersuchung). Zool. Jb. Anat. Bd. 86, 96-128.

Oh, J.K., Bohnsack, D.L., Troy, J.B., Enroth-Cugell, C., 1995. The cat's pupillary light response under urethane anesthesia. Visual Neurosci. 12(2), 281-284.

Ohtsuka, K., Asakura, K., Kawasaki, H. and Sawa, M., 1988. Respiratory fluctuations of the human pupil. Exp. Brain Res. 71(1), 215-217.

Okamoto, M., 1988. Fine structure of the iris muscle in the Japanese common newt, *Cynops pyrrhogaster*, with special reference to innervation. Zool. Sci. 5(2), 337-346.

Oliphant, L. W., Johnson, M. R., Murphy, C., Howland, H., 1983. The musculature and pupillary response of the great horned owl iris. Exp. Eye Res. 37, 583–595.

Ostrin, L.A., Garcia, M.B., Choh, V., Wildsoet, C.F., 2014. Pharmacologically stimulated pupil and accommodative changes in Guinea Pigs. Invest. Ophth. Vis. Sci. 55(8), 5456-5465.

Ott, M., Schaeffel, F., Kirmse, W., 1998. Binocular vision and accommodation in prey-catching chameleons. J. Comp. Physiol. A. 182(3), 319-330.

Ott, M., 2006. Visual accommodation in vertebrates: mechanisms, physiological response and stimuli. J. Comp. Physiol. A 192(2), 97-111.

Ouk, K., Hughes, S., Pothecary, C.A., Peirson, S.N., Morton, A.J., 2016. Attenuated pupillary light responses and downregulation of opsin expression parallel decline in circadian disruption in two different mouse models of Huntington's disease. Hum. Mol. Genet. 25(24), 5418-5432.

Owens, L., Buhr, E., Tu, D.C., Lamprecht, T.L., Lee, J., van Gelder, R.N., 2012. Effect of circadian clock gene mutations on nonvisual photoreception in the mouse. Invest. Ophth. Vis. Sci. 53(1), 454-460.

Packard, A., Sanders, G. D., 1971. Body patterns of *Octopus vulgaris* and the maturation of the response to disturbance. Anim. Behav. 19, 780-790.

Packard, A., 1972. Cephalopods and fish: the limits of convergence. Biol. Rev. 47(2), 241-307.

Panda, S., Provencio, I., Tu, D.C., Pires, S.S., Rollag, M.D., Castrucci, A.M., Pletcher, M.T., Sato, T.K., Wiltshire, T., Andahazy, M., Kay, S.A., van Gelder, R.N., Hogenesch, J.B., 2003. Melanopsin is required for non-image-forming photic responses in blind mice. Science 301, 525–527.

Pariente, G.F., 1979. The role of vision in prosimian behaviour, in: Doyle, G.A., Martin, R.D. (Eds.), The Study of Prosimian Behaviour. Academic Press, New York, pp. 411-459.

Perlman, I., Normann, A., 1998. Light adaptation and sensitivity controlling mechanisms in vertebrate photoreceptors. Prog. Retin. Eye Res. 17, 523-563.

Perganta, G., Barnard, A.R., Katti, C., Vachtsevanos, A., Douglas, R.H., MacLaren, R.E., Votruba, M., Sekaran, S., 2013. Non-image-forming light driven functions are preserved in a mouse model of autosomal dominant optic atrophy. PLoS One 8(2), p.e56350.

Petritz, O.A., Guzman, D.S.M., Gustavsen, K., Wiggans, K.T., Kass, P.H., Houck, E., Murphy, C.J., Paul-Murphy, J., 2016. Evaluation of the mydriatic effects of topical administration of rocuronium bromide in Hispaniolan Amazon parrots (*Amazona ventralis*). J. Am. Vet. Med. Assoc. 248(1), 67-71.

Pettigrew, J.D., Manger, P.R., Fine, S.L.B., 1998. The sensory world of the platypus. Philos. T. Roy. Soc. B 353(1372), 1199-1210.

Pilar, G., Nuňez, R., McLennan, I.S., Meriney, S.D. 1987. Muscarinic and nicotinic synaptic activation of the developing chicken iris. J. Neurosci. 7(12), 3813–3826.

Pong, M., Fuchs, A.F., 2000. Characteristics of the pupillary light reflex in the macaque monkey: Metrics. J. Neurophysiol. 84(2), 953-963.

Provencio, I., Jiang, G., de Grip, W.J., Hayes, W.P., Rollag, M.D., 1998. Melanopsin: An opsin in melanophores, brain, and eye. Proc. Natl. Acad. Sci. U.S.A. 95(1), 340-345.

Pyron, R.A., Wiens, J.J., 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. Mol. Phylogenet. Evol. 61(2), 543–583.

Rahi, A.H.S., Sheikh, H., Morgan, G., 1980. Histology of the camel eye. Acta Anat. 106, 345–350.

Raidal, S.R., 1997. Bilateral necrotizing pectenitis causing blindness in a rainbow lorikeet (*Trichoglossus haematodus*). Avian Pathol. 26(4), 871-876.

Ramer, J.C., Paul-Murphy, J., Brunson, D., Murphy, C.J., 1996. Effects of mydriatic agents in cockatoos, African gray parrots, and Blue-fronted Amazon parrots. J. Am. Vet. Med. Assoc. 208(2), 227-230.

Raselli, A., 1923. Morphologisches und Funktionelles über den Muskelapparat in der Iris der Katze. Graefes Arch. Clin. Exp. Ophthalmol. 111(3), 309-329.

Reger, J.F., 1966. The fine structure of iridial constrictor pupillae muscle of *Alligator mississippiensis*. Anat. Rec. 155, 197–215.

Rival, F., Linsart, A., Isard, P.F., Besson, C., Dulaurent, T. 2015. Anterior segment morphology and morphometry in selected reptile species using optical coherence tomography. Vet. Ophthalmol. 18 (suppl s1), 53-60.

Rivamonte, L.A., 2009. Bottlenose dolphin (*Tursiops truncatus*) double-slit pupil asymmetries enhance vision. Aquat. Mamm. 35(2), 269-280.

Roedel, M.O., Kosuch, J., Grafe, T.U., Boistel, R., Assemian, N.E., Kouamé, N.G., Tohe, B., Gourene, G., Perret, J.L., Henle, K., Tafforeau, P., 2009. A new tree-frog genus and species from Ivory Coast, West Africa (Amphibia: Anura: Hyperoliidae). Zootaxa 2044, 23-45.

Roper,T.J., Marples,N.M., 1997.Colour preferences of domestic chicks in relation to food and water presentation. Appl. Anim. Behav. Sci. 54, 207–213.

Roth, L.S.V., Balkenius, A., Kelber, A., 2008. The absolute threshold of colour vision in the horse. PLoS One, 3(11), e3711.

Roth, L.S.V., Lundstrom, L., Kelber, A., Kröger, R.H.H., Unsbo, P., 2009. The pupils and optical systems of gecko eyes. J. Vis. 9(3), article 27.

Rubin, L., Nolte, J., 1981. Autonomic innervation and photosensitivity of the sphincter pupillae muscle of two teleosts: *Lophius piscatorius* and *Opsanus tau*. Curr. Eye Res. 1(9), 543-551.

Rubin, L.J., Nolte, J.F., 1984. Modulation of the response of a photosensitive muscle by β-adrenergic regulation of cyclic AMP levels. Nature 307(5951), 551-553.

Rubin, L. J., Nolte, J.F., 1986. Cyclic nucleotide levels of the photosensitive irises of *Bufo marinus* and *Lophius*. Exp. Eye Res. 43(5), 771-779.

Rubin, L., Eller, P., Nolte, J., 1986. Fine structure of the photosensitive iris of the toad, *Bufo marinus*. J. Morphol. 188(2), 225-238.

Salzen, E. A., Lily, R. E., McKeown, J. R., 1971. Colour preferences and imprinting in domestic chicks. Anim. Behav.19, 542–547.

Scapolo, P. A., Peirone, S. M., Filogamo, G., Veggetti, A., 1988. Histochemical, immunohistochemical, and ultrastructural observation on the iris muscles of *Gallus gallus.* Anat. Rec. 221(3), 687–699.

Schaeffel, F., Howland, H. C., Farkas, L., 1986. Natural accommodation in the growing chicken. Vision Res. 26, 1977– 1993.

Schaeffel, F., de Queiroz, A., 1990. Alternative mechanisms of enhanced underwater vision in the garter snakes *Thamnophis melanogaster* and *T. couchii*. Copeia 1990(1), 50–58.

Schaeffel, F., Mathis, U., 1991. Underwater vision in semi-aquatic European snakes. Naturwissenschaften 78(8), 373-375.

Schaeffel, F., Wagner, H. G., 1992. Barn owls have symmetrical accommodation in both eyes but independent pupillary responses to light. Vision Res. 32, 1149–1155.

Schaeffel, F., Murphy, C. J., Howland, H. C., 1999. Accommodation in the cuttlefish (*Sepia officinalis*). J. Exp. Biol. 202, 3127–3134.

Schartau, J.M., Sjögreen, B., Gagnon, Y.L., Kröger, R.H.H., 2009. Optical plasticity in the crystalline lenses of the cichlid fish *Aequidens pulcher*. Curr. Biol. 19(2), 122-126.

Schiviz, A.N., Ruf, T., Kuebber-Heiss, A., Schubert, C., Ahnelt, P.K. 2008. Retinal cone topography of artiodactyl mammals: Influence of body height and habitat. J. Comp. Neurol. 507, 1336-1350.

Schmid, K.L., Howland, H.C., Howland, M.J., 1992. Focusing and accommodation in tuatara (*Sphenodon punctatus*). J. Comp. Physiol. A 170, 263–266.

Schmidt, T.M., Rupp, A.C., Chew, K.S., Yungher, B., Cui, Y., Wess, J., Park, K., Hattar, S., 2014. A retinal projection to the iris mediates pupil constriction. Invest. Ophth. Vis. Sci. 55(13), 1231-1231.

Schusterman, R.J., Balliet, R.F., 1971. Aerial and underwater visual acuity in the California sea lion (*Zirlophus californianus*) as a function of luminance. Ann. N.Y. Acad. Sci. 188, 37-46.

Seggie, J., Steiner, M., Wright, N., Orpen, G., 1989. The effect of lithium on pupillary response to pulses of light in sheep. Psychiat. Res. 30(3), 305-311.

Seliger, H.H., 1962. Direct action of light in naturally pigmented muscle fibres I. Action spectrum for contraction in eel iris sphincter. J. Gen. Physiol. 46, 333-342.

Semo, M., Gias, C., Ahmado, A., Vugler, A., 2014. A role for the ciliary marginal zone in the melanopsin-dependent intrinsic pupillary light reflex. Exp. Eye Res. 119, 8-18.

Simões, B.F., Gower, D.J., 2017. Visual pigment evolution in reptiles. in: eLS. John Wiley & Sons Ltd, Chichester.

Sipe, G.O., Dearworth, J.R., Selvarajah, B.P., Blaum, J.F., Littlefield, T.E., Fink, D.A., Casey, C.N., McDougal, D.H., 2011. Spectral sensitivity of the photointrinsic iris in the red-eared slider turtle (*Trachemys scripta elegans*). Vision Res. 51(1), 120-130.

Sivak, J.G., 1978. The functional significance of the aphakic space of the fish eye. Can. J. Zool. 56(3), 513-516.

Sivak, J.G., 1979. Accommodative lens movements and pupil shape in teleost fishes. Israel J. Zool. 28(4), 218-223.

Sivak, J.G., 1980. Accommodation in vertebrates: a contemporary survey. Current Topics in Eye Research 3, 281-330.

Sivak, J. G., Howland, H. C., McGill-Harelstad, P., 1987. Vision of the Humboldt penguin (*Spheniscus humboldti*) in air and water. P. Roy. Soc. Lond. B Bio. 229, 647-472.

Sivak, J. G., Howland, H. C., West, J., Weerheim, J., 1989. The eye of the hooded seal, *Cystophora cristata*, in air and water. J. Comp. Physiol. A 165, 771-777.

Sivak, J.G., 1990. Optical variability of the fish lens, in: Douglas, R.H., Djamgoz, M.B.A. (Eds.), The Visual System of Fish. Chapman & Hall, London, pp. 63-80

Sivak, J.G., 1991. Elasmobranch visual optics. J. Exp. Zool. Suppl. 5, 13-21.

Sivak, J.G., Luer, C.A., 1991. Optical development of the ocular lens of an elasmobranch, *Raja elanteria*. Vision Res. 31(3), 373-382.

Smith, S.A., Ellis, C.J., Smith, S.E., 1979. Inequality of the direct and consensual light reflexes in normal subjects. Brit. J. Ophthalmol. 63(7), 523-527.

Somiya, H., 1987. Dynamic mechanism of visual accommodation in teleosts: structure of the lens muscle and its nerve control. P. Roy. Soc. Lond. B Bio. 230(1258), 77-91.

Staflova, J., 1969. A comparative study of the adrenergic innervation of the iris and ciliary structures in 18 species in phylogenesis. J. Morphol. 128, 387-402.

Steinach, E., 1890. Untersuchungen zur vergleichenden Physiologie der Iris. Pflügers Arch. Ges. Physiol. 47, 289-340.

Steinach, E., 1892. Untersuchungen zur vergleichenden Physiologie der Iris. Pflügers Arch. Ges. Physiol. 52, 495-525.

Steinhauer, S.R., Siegle, G.J., Condray, R., Pless, M., 2004. Sympathetic and parasympathetic innervation of pupillary dilation during sustained processing. Int. J. Psychophysiol. 52, 77–86.

Stubbs, A.L., Stubbs, C.W., 2016a. Spectral discrimination in color blind animals via chromatic aberration and pupil shape. Proc. Natl. Acad. Sci. U.S.A. 113(29), 8206–8211.

Stubbs, A.L., Stubbs, C.W., 2016b. All color vision is more difficult in turbid water. Proc. Natl. Acad. Sci. U.S.A. 113(45), E6910-E6910.

Studnitz, G. von, 1932a. Beträge zur Adaptation der Teleosteer. Studien zur vergleichenden Physiologie der Iris II. Z. vergl. Physiol. 18(2), 307-338.

Studnitz, G. von, 1932b. Studien zur vergleichenden Physiologie der iris. I. *Rana temporaria*. Pflügers Arch. Ges. Physiol. 229(1), 492-537.

Studnitz, G. von, 1933. Studien zur vergleichenden Physiologie der Iris III. Selachier. Z. vergl. Physiol. 19, 619-681.

Suzuki, R., Yoshino, H., Kurimoto, S., 1991. Effects of ultraviolet radiation and visible light on hamster pupil. Doc. Ophthalmol. 77(1), 81-87.

Talbot, C.M., Marshall, N.J., 2010. Polarization sensitivity and retinal topography of the striped pyjama squid (*Sepioloidea lineolata* – Quoy/Gaimard 1832). J. Exp. Biol. 213, 3371-3377.

Talbot, C.M., Marshall, N.J., 2011. The retinal topography of three species of coleoid cephalopod: significance for perception of polarized light. Philos. T. Roy. Soc. B 366(1565), 724-733.

The World Conservation Union, 2014. IUCN Red List of Threatened Species, version 2014.3: Table 1.

Thompson, S., Whiting, R.E., Kardon, R.H., Stone, E.M., Narfström, K., 2010. Effects of hereditary retinal degeneration due to a CEP290 mutation on the feline pupillary light reflex. Vet. Ophthalmol. 13(3), 151-157.

Trejo, L. J., Rand, M. N., Cicerone, C. M., 1989. Consensual pupillary light reflex in the pigmented rat. Vision Res. 29, 303-309.

Tu, D.C., Batten, M.L., Palczewski, K.,van Gelder, R.N., 2004. Nonvisual photoreception in the chick iris. Science 306, 129–131.

Tyler, M.J., Davies, M., 1978. Phylogenetic relationships of Australian hyline and neotropical phyllomedusine frogs of the family Hylidae. Herpetologica, 34(2), 219-224.

Underwood, G., 1951. Pupil shape in certain gekkos. Copeia 3, 211-212.

Underwood, G., 1954. The classification and evolution of gekkos. Proc. Zool. Soc. Lond. 124, 469-492.

Valdez, D.J., Nieto, P.S., Garbarino-Pico, E., Avalle, L.B., Díaz-Fajreldines, H., Schurrer, C., Cheng, K.M., Guido, M.E., 2009. A non-mammalian vertebrate model of blindness reveals functional photoreceptors in the inner retina. FASEB J. *23*(4), 1186-1195.

Valdez, D.J., Nieto, P.S., Della Costa, N.S., Schurrer, C., Guido, M.E., 2015. Circadian control of the pupillary light responses in an avian model of blindness, the GUCY1* chickens. Invest. Ophth. Vis. Sci. 56(2), 730-737.

Volpe, P., Biral, D., Pizzo, P., Salviati, G., Margreth, A., 1993. Ontogenesis of chick iris intrinsic muscles: Evidence for a smooth-to-striated transition. Dev. Biol. 159, 441–449.

Vugler, A., Semo, M., Ortín-Martínez, A., Rojanasakul, A., Nommiste, B., Valiente-Soriano, F.J., García-Ayuso, D., Coffey, P., Vidal-Sanz, M., Gias, C., 2015. A role for the outer retina in development of the intrinsic pupillary light reflex in mice. Neuroscience 286, 60-78.

Wagner, H.-J., Kirsch, M., Douglas, R. H., 1992. Light dependent and endogenous circadian control of adaptation in teleost retinae, in: Ali, M.A. (Ed.), Rhythms in Fishes. Plenum Press, New York, pp. 255-291.

Wake, M.H., 1985. The comparative morphology and evolution of the eyes of caecilians (Amphibia, Gymnophora). Zoomorphology 105(5), 277-295.

Walls, G.L., 1942. The Vertebrate Eye and its Adaptive Radiation. The Cranbrook Press, Bloomington Hills.

Ward, R., Repérant, J., Hergueta, S., Miceli, D., Lemire, M., 1995. Ipsilateral visual projections in non-eutherian species: random variation in the central nervous system? Brain Res. Rev. 20, 155–170.

Warrant, E. J., McIntyre, P. D., 1996. The visual ecology of pupillary action in superposition eyes. J. Comp. Physiol. A 178, 75–90.

Warrant, E.L., Locket, N.A., 2004. Vision in the deep sea. Biol. Rev. 79, 671–712.

Watanabe, T., Koike, N., Inoue, T., Kondo, Y., Yanagaki, H., Yasuda, T., 1990. An automated simultaneous recording system for the pupillary movement and unitary discharge of the ciliary nerve in cats. Jpn. J. Appl. Phys. *29*(2R), 445-452.

Weale, R.A., 1956. Observations on the direct effect of light on the irides of *Rana temporaria* and *Xenopus laevis*. J. Physiol. 132(2), 257-266.

Weel, P. B. V., Thore, S., 1936. Über die Pupillarreaktion von *Octopus vulgaris*. Z. vergl. Physiol. 23, 26-33.

Wells, M.J., 1960. Proprioception and visual discrimination of orientation in *Octopus*. J. Exp. Biol. 37(3), 489-499.

Wells, M.J., 1966. Cephalopod sense organs, in: Wilbur, C.M., Yonge, C.M. (Eds.), Physiology of Mollusca, 2. Academic Press, New York, pp. 523-545.

Wells, M. J., 1978. Octopus; Physiology and Behaviour of an Advanced Invertebrate. Chapman and Hall, London.

Werner, D., 1972. Beobachtungen an *Ptyodactylus hasselquistii guttatus* (Geckonidae). Verh. Naturforsch. Ges. Basel 82, 54-87.

Werner, Y.L. 1967. Dark adaptation of the vertical pupil in a snake. Herpetologica 23 (1), 62–63.

Werner, Y. L., 1969. Eye size in geckos of various ecological types (reptilia: Gekkonidae and sphaerodactylidae). Israel J. Zool. 18, 291–316.

Werner, Y.L., 1970. Extreme adaptability to light, in round pupil of snake spalerosophis. Vision Res. 10(11), 1159-1164.

West, J.A., Sivak, J.G., Murphy, C.J., Kovacs, K.M., 1991. A comparative study of the anatomy of the iris and ciliary body in aquatic mammals. Can. J. Zool. 69(10), 2594-2607.

Whiting, R.E., Yao, G., Narfström, K., Pearce, J.W., Coates, J.R., Dodam, J.R., Castaner, L.J., Katz, M.L., 2013. Quantitative assessment of the canine pupillary light reflex. Invest. Ophth. Vis. Sci. 54(8), 5432-5440.

Wilcox, J.G., Barlow, H.B. 1975. The size and shape of the pupil in lightly anaesthetized cats as a function of luminance. Vision Res. 15, 1363-1365.

Wilhelm, H., Lüdtke, H., Wilhelm, B., 1998. Pupillographic sleepiness testing in hypersomniacs and normals. Graefes Arch. Clin. Exp. Ophthalmol. 236(10), 725-729.

Willigen, R.F. van der, Frost, B.J., Wagner, H., 1998. Stereoscopic depth perception in the owl. Neuroreport 9, 1233–1237.

Wilson G., 1970. Some comments on the optical systems of pinnipedia as a result of observations on the Weddell seal (*Leptonychotes weddelli*). British Antarctic Survey Bulletin 23, 57–62.

Wolin, L.R., Massopust Jr, L.C., 1967. Characteristics of the ocular fundus in primates. J. Anat. 101(4), 693-699.

Xue, T., Do, M.T.H., Riccio, A., Jiang, Z., Hsieh, J., Wang, H.C., Merbs, S.L., Welsbie, D.S., Yoshioka, T., Weissgerber, P., Stolz, S., 2011. Melanopsin signalling in mammalian iris and retina. Nature 479(7371), 67-73.

Yamashita, T., Sohal, G.S., 1986. Development of smooth and skeletal muscle cells in the iris of the domestic duck, chick and quail. Cell Tissue Res. 244(1), 121-131.

Yeh, C.Y., Koehl, K.L., Harman, C.D., Iwabe, S., Guzman, J.M., Petersen-Jones, S.M., Kardon, R.H., Komáromy, A.M., 2017. Assessment of rod, cone, and intrinsically photosensitive retinal ganglion cell contributions to the canine chromatic pupillary response. Invest. Ophth. Vis. Sci. 58(1), 65-78.

Young, J.Z., 1931. The pupillary mechanism of the teleostean fish, *Uranoscopus scaber.* P. Roy. Soc. Lond. B Bio. 107, 464-485.

Young, J.Z., 1933a. Comparative studies of the physiology of the iris. - I. Selachians P. Roy. Soc. Lond. B Bio. 112, 228-241.

Young, J.Z., 1933b. Comparative studies of the physiology of the iris. - II. *Uranoscopus* and *Lophius.* P. Roy. Soc. Lond. B Bio. 112, 242-249.

Young, R. E., 1978. Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. Fish Bul. 76(3), 583-615.

Young, R. S. L., Kimura, E., 2008. Pupillary correlates of light-evoked melanopsin activity in humans. Vision Res. 48, 862–871.

Zenker, W., Krammer, E., 1967. Untersuchungen über Feinstruktur und Innervation der inneren Augenmuskeln des Huhnes. Z. Zellforsch. Mikrosk. Anat. 83, 147–168.

Zucker, R., Nolte, J., 1978. Light-induced calcium release in a photosensitive vertebrate smooth muscle. Nature 274, 78-80.

Zucker, R.M., Nolte, J., 1981. A search for the photoreceptor in the photosensitive iris of normally pigmented and albino hamsters (*Mesocricetus auratus*). Curr. Eye Res. 1, 9-27.

Zusi, R.L., Bridge, D., 1981. On the slit pupil of the Black skimmer (*Rynchops niger*). Herpetologica 52(4), 338-340.

Figure 1 Toluidine blue stained sections of human iris.
(A) Lower power micrograph of the whole iris. (B)&(C) higher power micrographs showing the sphincter and dilator muscles, respectively. C-cornea; CB-ciliary body; ABL-anterior border layer; S-stroma; PM-pupil margin; SP-sphincter pupillae muscle; PE-posterior pigment epithelium; DP-dilator pupillae muscle.

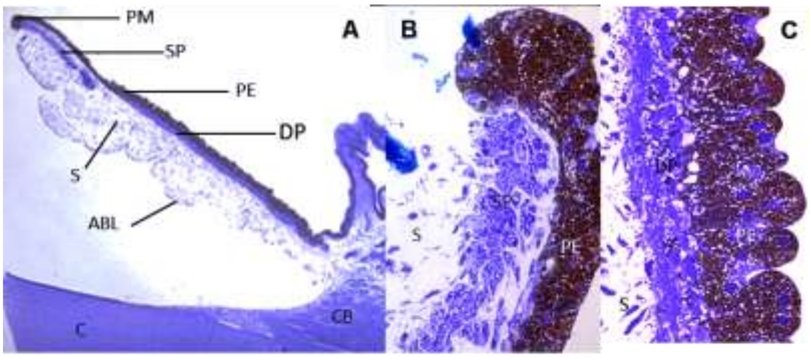

Figure 2 Iris muscles in animals with different pupil shapes.
(A) shows the circumerfential sphincter muscle typical of animals with circular pupils. (B) illustrates the two crossing sphincter bundles in a slit pupil. (C) shows the sphincter fibres in an animal with a rectangular pupil, most of which are circular but some sphincter fibres are orientated radially and anchored to connective tissue (stippled area). In all irises the dilator muscles are radial (from Walls, 1942).

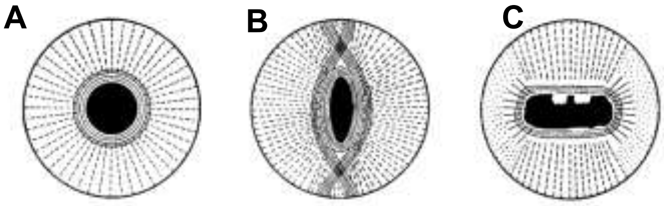

Figure 3 Wholemount of zebra fish (*Danio rerio*) iris stained with phalloidin coupled to alexa488, viewed under (blue) fluorescence. This shows filamentous actin and reveals staining consistent with the presence of a sphincter and dilator muscle in the iris of a species whose pupils are static (Wagner & Douglas, unpubl).

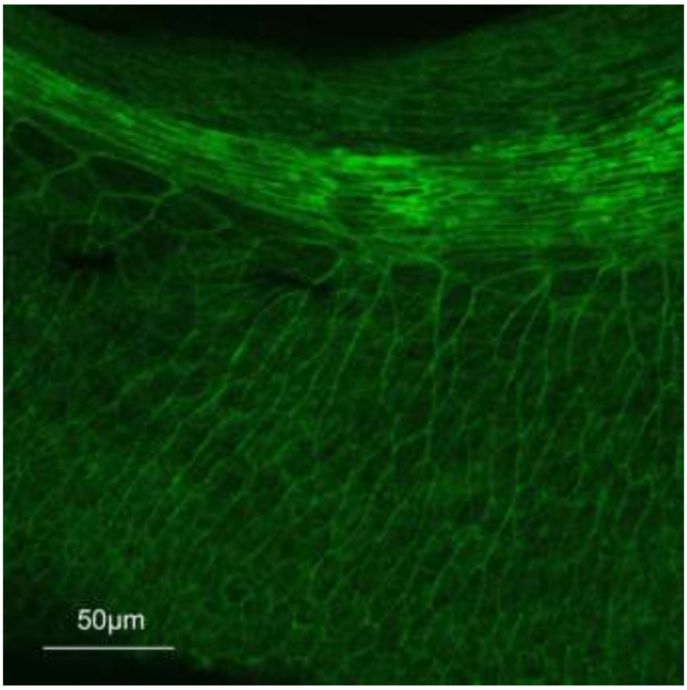

Figure 4 Mammalian pupil shape
(A) The partially constricted and (B) constricted vertical slit pupil of a cat (*Felis catus*), which is typical of many carnivores (SL Douglas). (C) Constricted pupil of a bottlenose dolphin (*Tursiops truncatus*), where the dorsal operculum has occluded most of the pupil leaving only a small rostral aperture and a larger temporal gap (from Rivamonte, 2009). The pupil of the horse (*Equus ferus caballus*) in (D) moderate and (E) high light levels respectively. In the partially constricted, horizontally rectangular pupil, typical of many ungulates, the superior corpora nigra is clearly visible intruding into the pupil. In the fully constricted pupil, the corpora nigra reaches the inferior pupil margin, forming 2 small apertures (from Miller & Murphy, 2016).

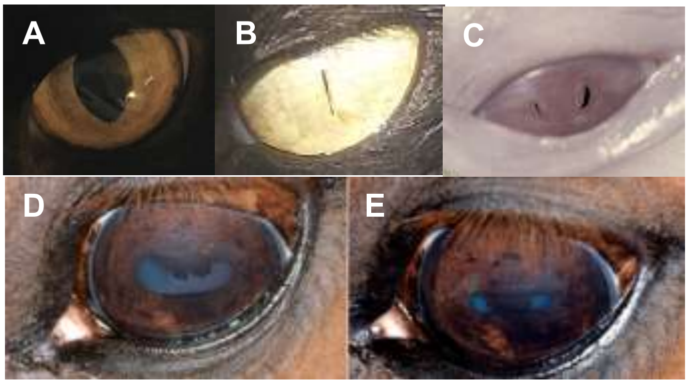

Figure 5 Human pupillary light reflexes in response to varying levels of illumination.
(A)-(C) show responses to 1sec monocular flashes of white light of 3 different intensities in the stimulated (solid line) and unstimulated (dashed line) eye. Periods of light are outlined by the double arrows. (D) shows the responses of the stimulated eye to 3 different intensities of prolonged illumination. The divisions on the abscissa represent 0.1 secs (modified from Lowenstein & Loewenfeld, 1959).

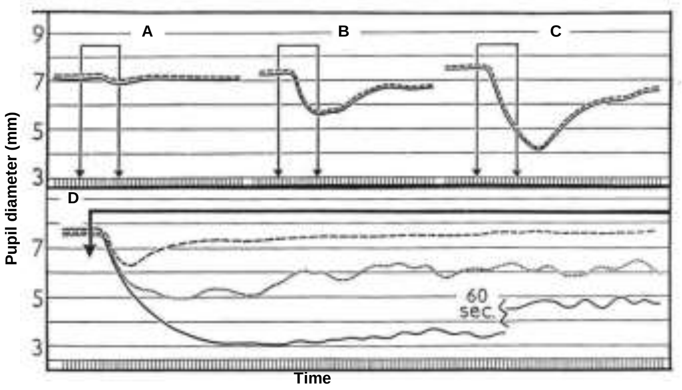

Figure 6 Pupil area as a function of luminance in humans and chickens (*Gallus gallus domesticus*).
Human data are indicated by the dashed line and those of chickens by the solid line. Data are taken from Barbur et al (2002), where experimental details can be found.

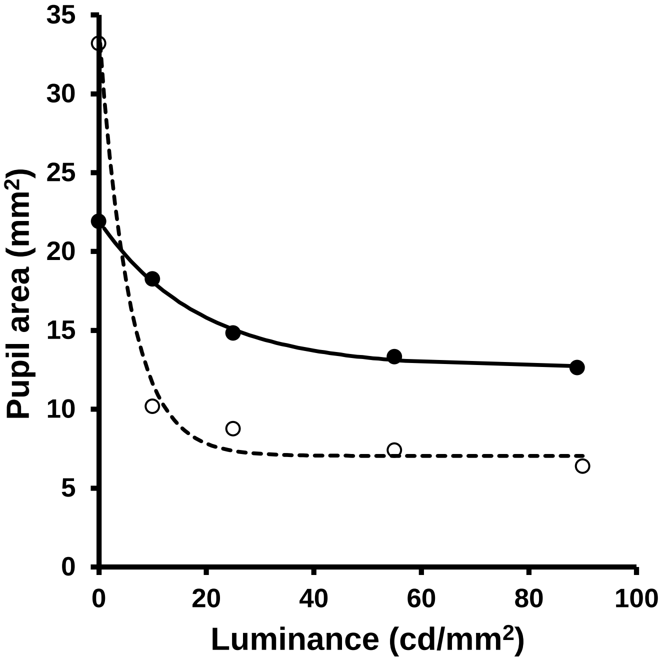

Figure 7 Degree of pupil constriction as a function of light level in blue fronted parrots (*Amazona aestival*), snowy owls (*Bubo scandiacus*), and cats (*Felis catus*).

The parrots (solid line) require most illumination for constriction and the cats (triangles) least. The cat pupil constricts to a greater degree than the bird pupils (from Lind et al., 2008).

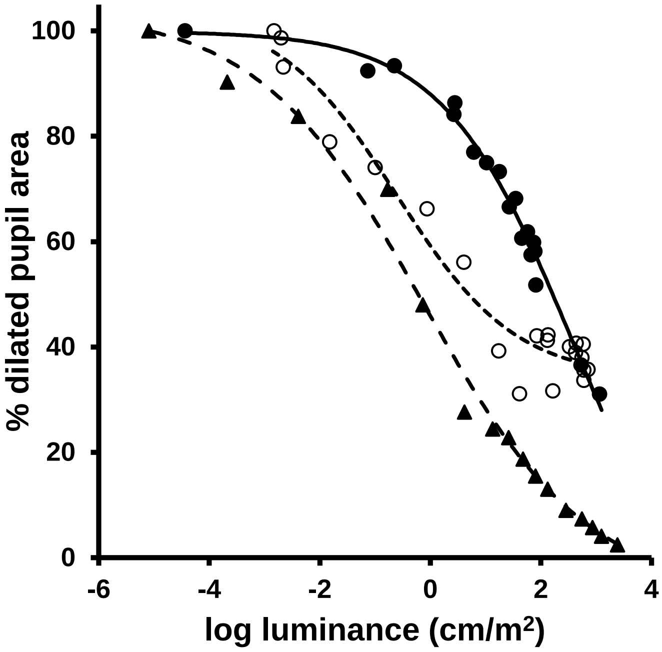

Figure 8 Changes in pupil size in humans and chickens (*Gallus gallus domesticus*) in response to simple changes in light flux and isoluminant red light stimulation.

Human data are indicated by the dashed lines and those of chickens by the solid lines. Reponses to changes in light flux are indicated by the black curves and the red curves represent responses to red light. Data are taken from Barbur et al (2002), where experimental details can be found. The duration of the 0.5sec stimulus is indicated by the vertical dotted grey lines. The red stimulus was rendered isoluminant by being buried in dynamic luminance contrast noise.

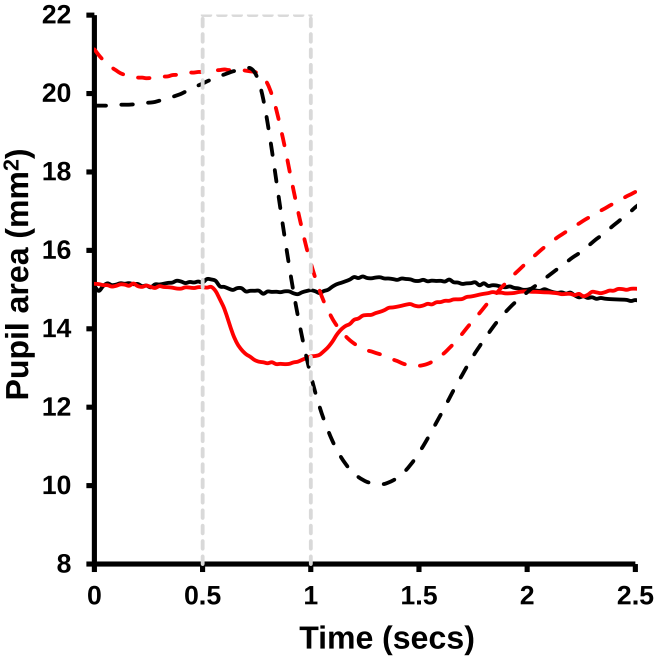

Figure 9 Pupils of helmet geckos (*Tarentola chazaliae*).
in different light intensities.
(A) Pupil area as a function of light intensity. (B)&(C) Pictures of fully dilated and constricted pupils (from Roth et al., 2009).

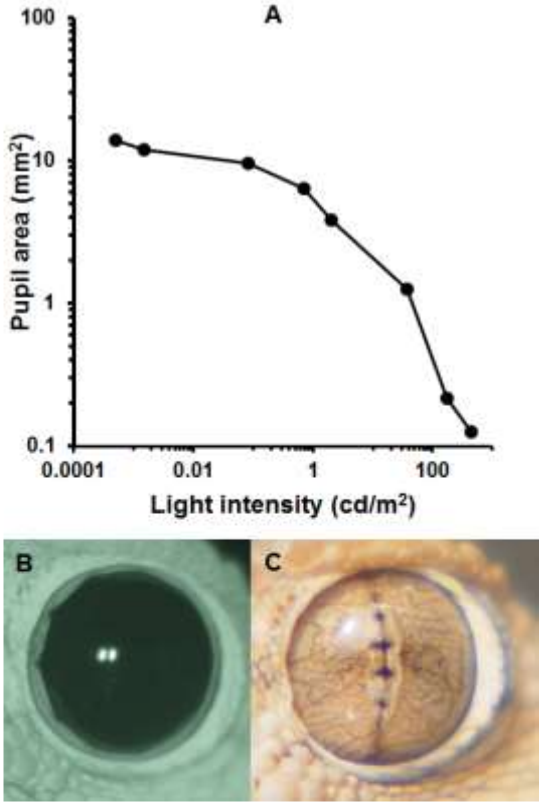

Figure 10 Constricted pupil shapes of various frogs.
(A)-(D) *Bombinator pachypus*, (E) *Alytes obstetricians*, (F) *Pelobates fuscus*, (G) *Rana arvalis*., (H) *Bufo vulgaris* (from Mann, 1931).

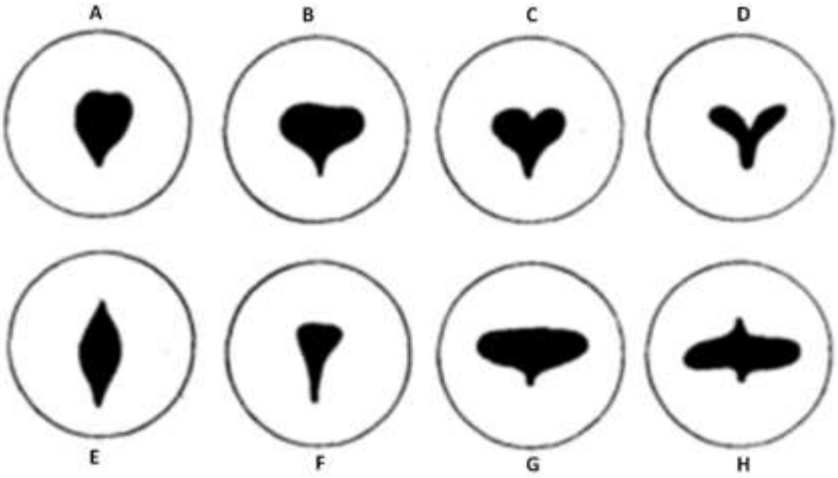

Figure 11 Pupil area of the right eye of a single unrestrained common frog (*Rana temporaria*) following various exposures to 501nm light.
In order of increasing effectiveness the intensities of the exposures were; $2.43\text{x}10^{-1}$ μW/cm^2; $9.98\text{x}10^{-1}$ μW/cm^2; 2.79 μW/cm^2; 4.77 μW/cm^2 (dotted); $1.41\text{x}10^{1}$ μW/cm^2 (dotted); $1.65\text{x}10^{1}$ μW/cm^2; $2.44\text{x}10^{1}$ μW/cm^2; $5.01\text{x}10^{1}$ μW/cm^2. A minimum of 5mins in darkness elapsed between successive light stimuli. The variable duration of the responses is due to movement of the animal (Douglas, unpubl).

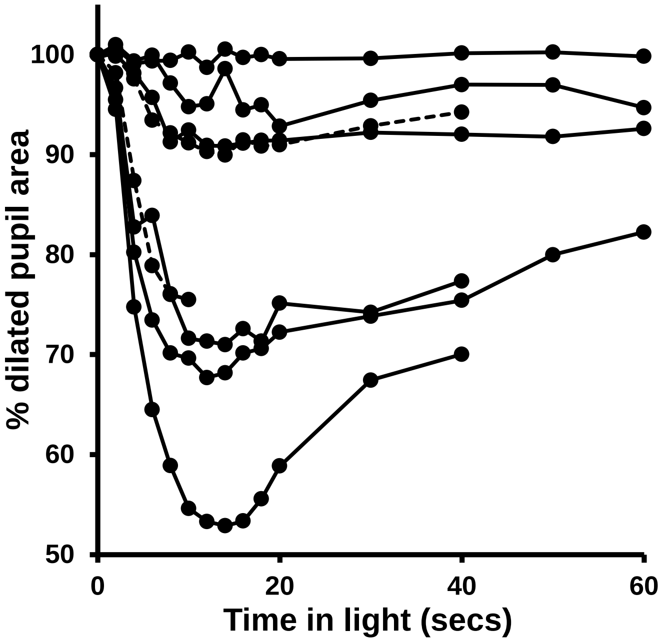

Figure 12 Pupil area of the right eye of a single unrestrained African clwed frog (*Xenopus laevis*) following various exposures to 501nm light.
In order of increasing effectiveness the intensities of the exposures were; $3.00x10^{-1}$ µW/cm^2; 4.77 µW/cm^2; $1.41x10^1$ µW/cm^2; $1.65x10^1$ µW/cm^2; $5.01x10^1$ µW/cm^2. The final, and most effective, response was following intense white light illumination ($3.39x10^3$ µW/cm^2; dotted line). A minimum of 14mins in darkness elapsed between successive light stimuli (Douglas, unpubl).

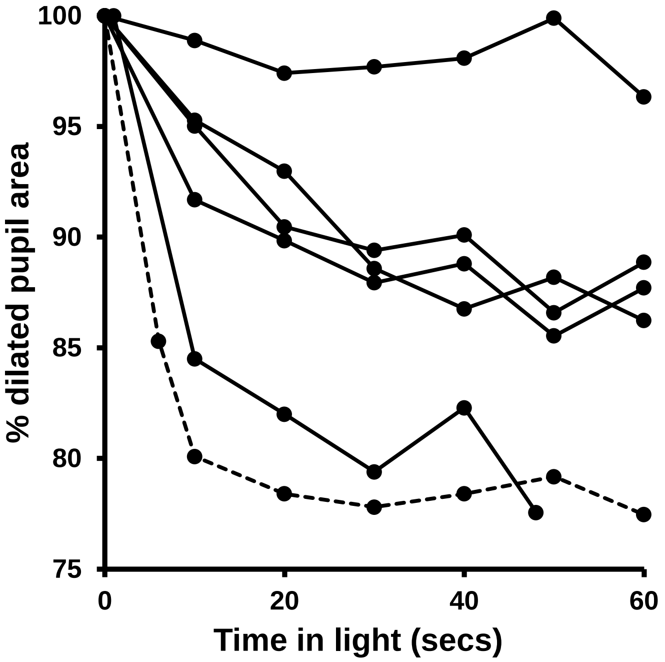

Figure 13 Infrared images of pupils from 3 species of fish in darkness (left) and after light exposure (right).
(A)&(B) The swellshark (*Cephaloscyllium ventriosum*), whose constricted pupil is a slanted horizontal slit with 2 pinholes at either end. (C)&(D) The plainfin midshipman (*Porichthys notatus*), whose pupil consists of 2 small apertures on light adaptation. (E)&(F) The armoured catfish (*Liposarcus pardalis*), with a horseshoe-shaped constricted pupil. Dorsal is at the top of the figures and rostral on the right (images A-D from Douglas et al.1998; E&F from Douglas et al., 2002).

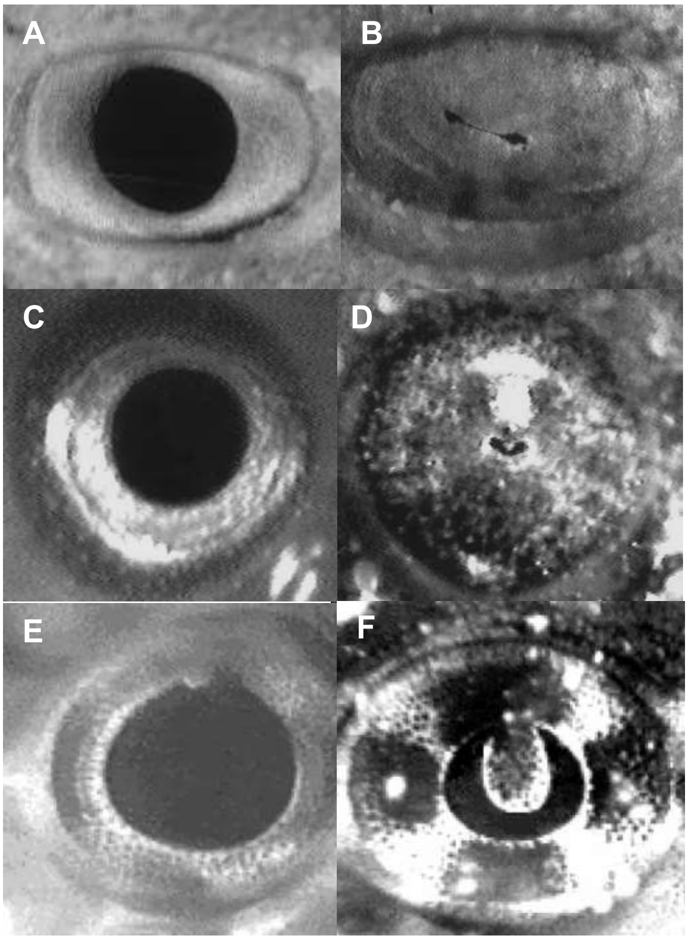

Figure 14 Irregular pupils with dorsal operculae in various bottom dwelling fish.
(A) bluespotted ray (*Neotrygon kuhlii*), (B) Eastern shovelnose ray (*Aptychotrema rostrate*), (C) crocodile fish (*Cymbacephalus beauforti*), (D) false stone fish (*Scorpaenopsis diabolus*) (NJ Marshall).

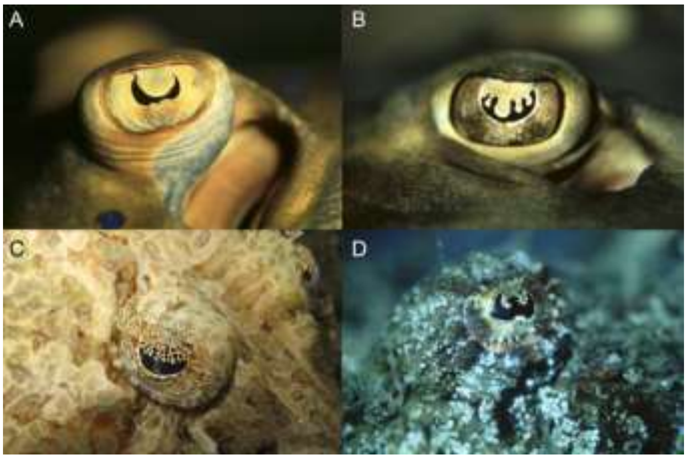

Figure 15 Pupil response of a swell shark (*Cephaloscyllium ventriosum*) and a plainfin midshipman (*Porichthys notatus*) in response to prolonged exposure to a bright (6.75x10^4 µW/cm^2) white light.
The swellshark is shown by the dashed line and triangles. The fully dilated pupil areas of the elasmobranch and teleost pupil were 7.78mm^2 and 4.73mm^2 respectively (from Douglas et al., 1998).

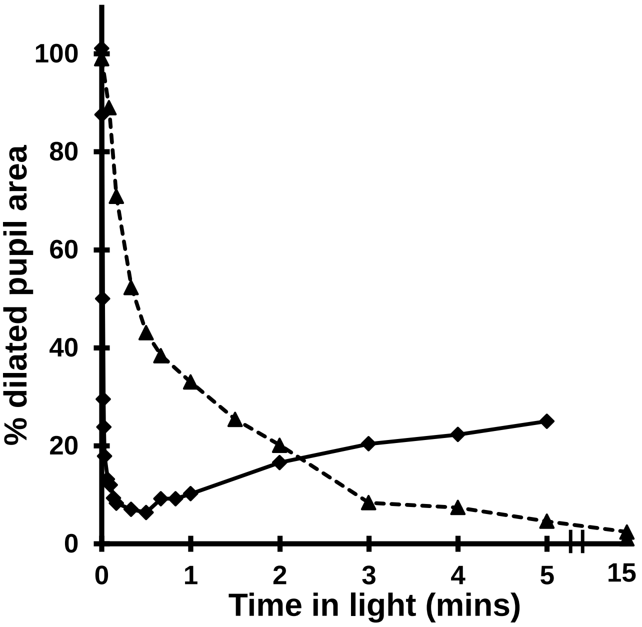

Figure 16 Pupil responses of an individual plainfin midshioman (*Porichthys notatus*) during 30 seconds exposure to different intensities of 501nm light. In order of the degree of constriction after 30 secs light exposure, intensities are; complete darkness, 2.72x10^{-3} μW/cm^2, 1.44x10^{-2} μW/cm^2, 7.07x10^{-2} μW/cm^2, 2.14x10^{-1} μW/cm^2, 2.71x10^{-1} μW/cm^2, 2.85 μW/cm^2 (dashed), 3.27x 0^2 μW/cm^2. Also shown is the response to maximum intensity (6.75x10^4 μW/cm^2) white light exposure (from Douglas et al., 1998).

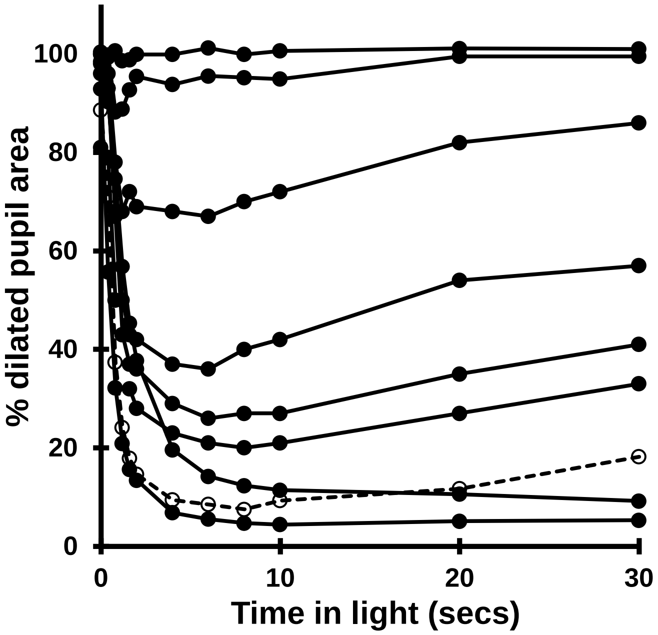

Figure 17 Pupil response of an individual armoured catfish (*Liposarcus pardalis*) during 60 minutes exposure to different intensities of white light. In order of increasing effectiveness, these are; complete darkness, 8.4x10^{-2} µW/cm^{2}, 1.37 µW/cm^{2}, 4.6x10^{1} µW/cm^{2}, 2.65x10^{2} µW/cm^{2} , 5.6x10^{3} µW/ cm^{-2} (from Douglas et al., 2002).

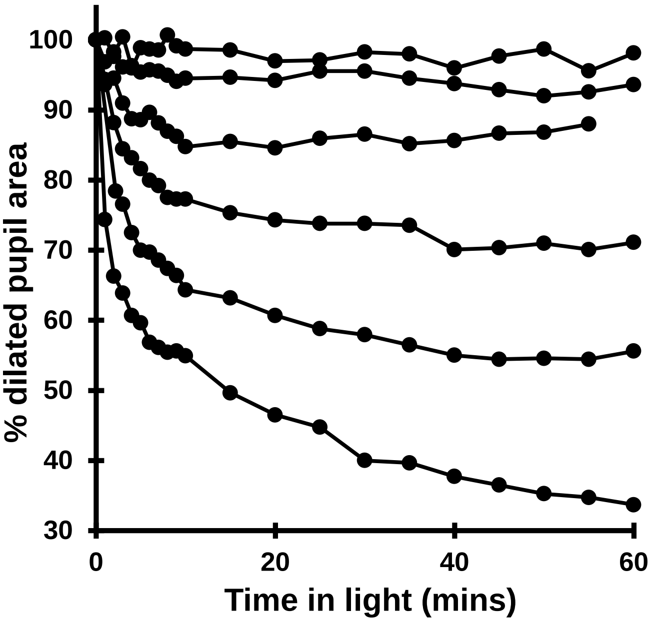

Figure 18 Cephalopod pupils

(A) Partially constricted pupil of an octopus (*Abdopus aculetus*) forming a horizontal rectangle (R Caldwell).

(B) Fully constricted pupil of an octopus (*Callistoctopus aspilosomatis*) consisting of 2 pinholes at either end of a horizontal slit (R Caldwell).

(C) Constricted 'horseshoe-shaped' pupil of a squid (*Loligo sp.*) (NJ Marshall).

(D) Partially constricted and (E) constricted pupil of a cuttlefish (*Sepia officinalis)*.

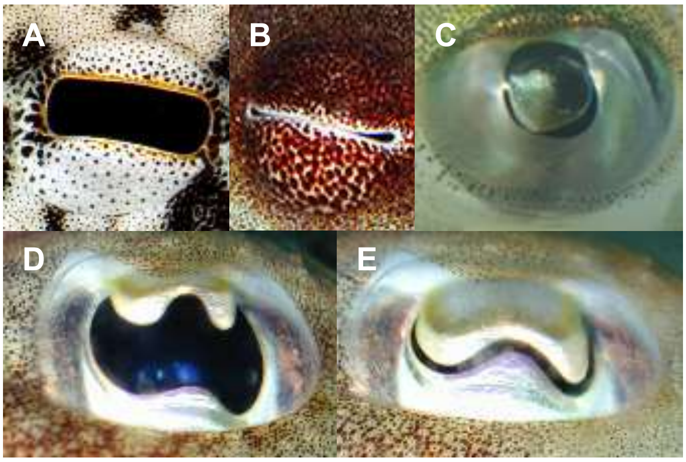

Figure 19 Relative pupil area of 3 species of cephalopod after exposure to white light.

Common cuttlefish (*Sepia officinalis*) (189 µW/cm^2 ; solid line; Douglas et al., 2005), striped pyjama squid (*Sepioloidea lineolate*) (15 µW/cm^2; dotted line; Partridge, White & Douglas, unpubl) and curled octopus (*Eledone cirrhosa*) (445 µW/cm^2; dashed line; Douglas et al., 2005)

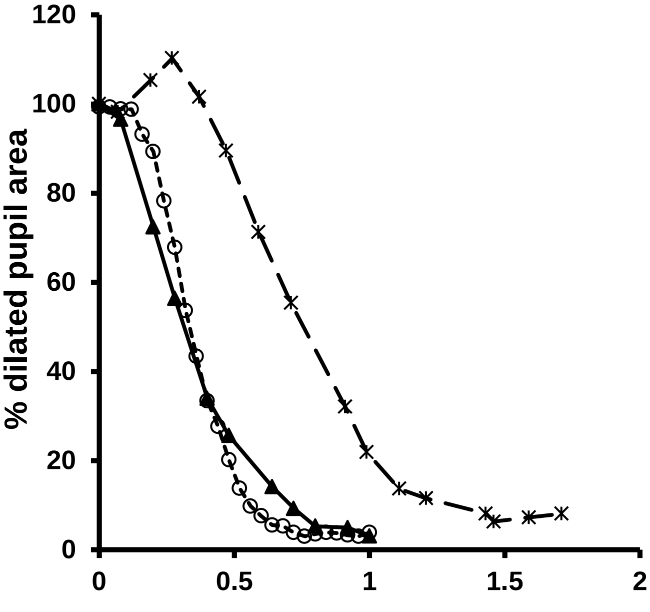

Figure 20 Relative pupil area of a deepsea octopus (*Japetella diaphana*) after exposure to bright white light.

Responses of 2 animals, with mantle lengths 27mm and 36mm represented by the solid and open symbols respectively, are shown. Animals were caught off the coast of Guatamala and kept in darkness at 4ºC for 12-18hrs before light exposure (Douglas, unpubl).

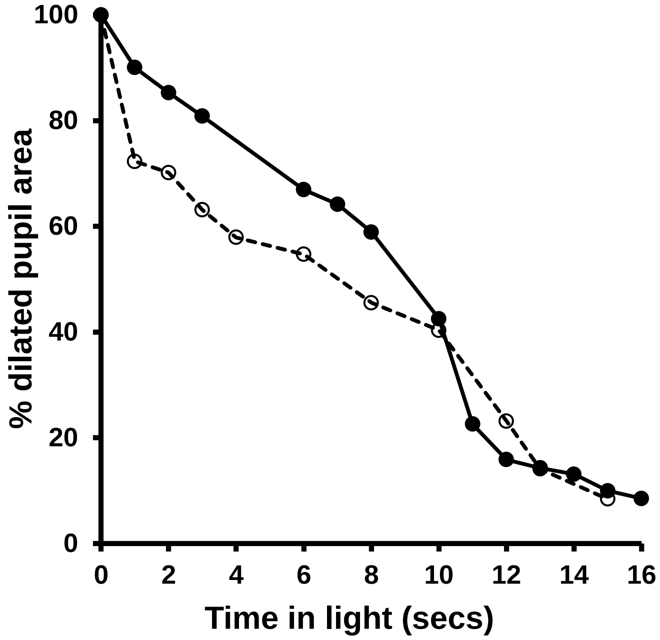

Figure 21 Pupil light responses of wild-type and rodless-coneless (rd/rd cl) mice (*Mus musculus*).
Dark adapted mice were exposed continuously to bright white light (3mW/cm^2). The wild type animals are shown by the dotted line and open circles. Areas are the mean for 6 mice per genotype (from Lucas et al., 2001).

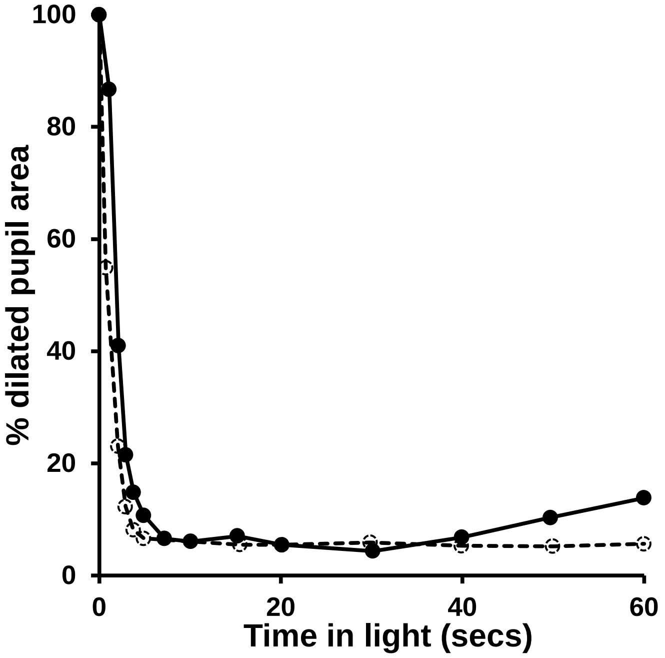

Figure22 Schematic representation of the parasympathetic and sympathetic innervation of the primate iris (from McDougal & Gamlin, 2015).

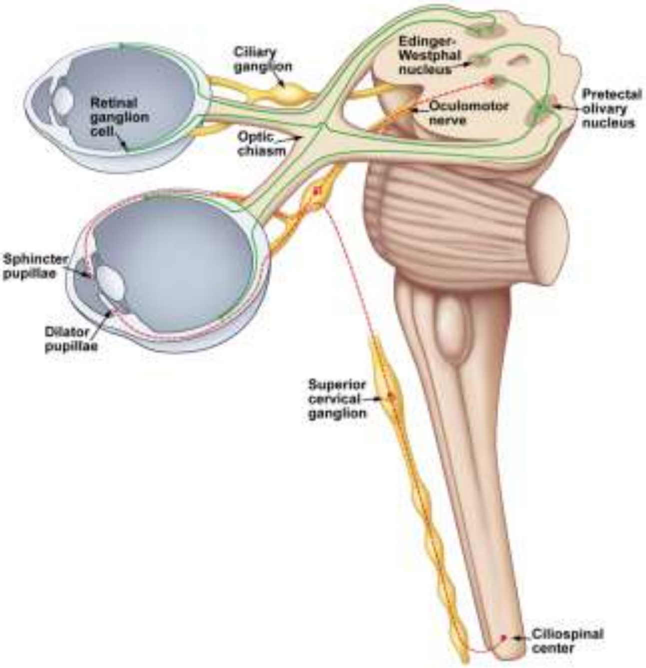

Figure 23 Pupil area of an isolated common frog (*Rana temporaria*) eye following various exposures to 501nm light.
In order of increasing effectiveness at 60mins the intensities of the exposures were; 2.43x10^{-1} µW/cm^2, 9.98x10^{-1} µW/cm^2, 4.77 µW/cm^2 (dashed), 2.79 µW/cm^2, 1.65x10^1 µW/cm^2, 2.44x10^1 µW/cm^2, 1.41x10^1 µW/cm^2 (dashed), 5.01x10^1 µW/cm^2. A minimum of 5mins in darkness elapsed between successive light stimuli (Douglas, unpubl).

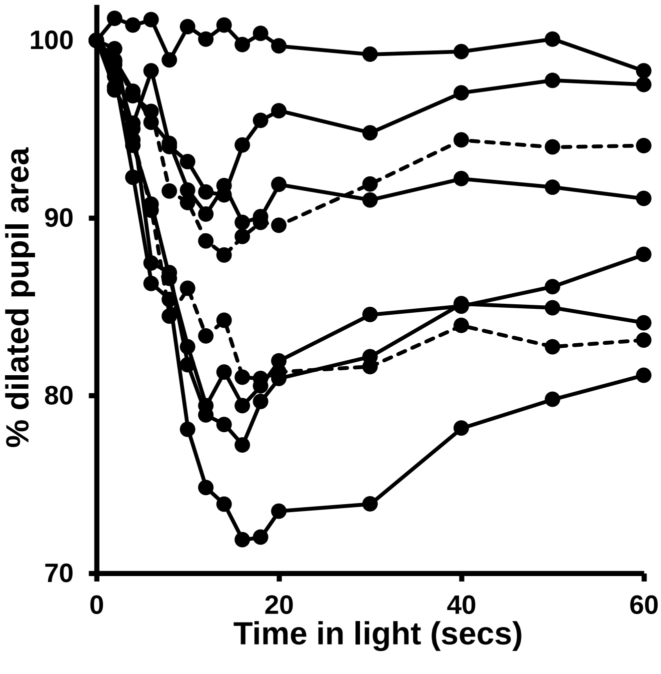

Figure 24 Body patterns on teleost fish that serve to conceal the location of the eye.
(A) weedy scorpionfish (*Rhinopias aphanes*), (B) blue surgeonfish (*Paracenthurus hepatus*), (C) flying gurnard (*Dactyloptena orientalis*), (D) juvenile boxfish (*Ostracion cubicus*), (E) butterflyfish (*Chaetodon ulietensis*), (F) juvenile angelfish (*Pomacanthus imperator*) (S Parish & NJ Marshall).

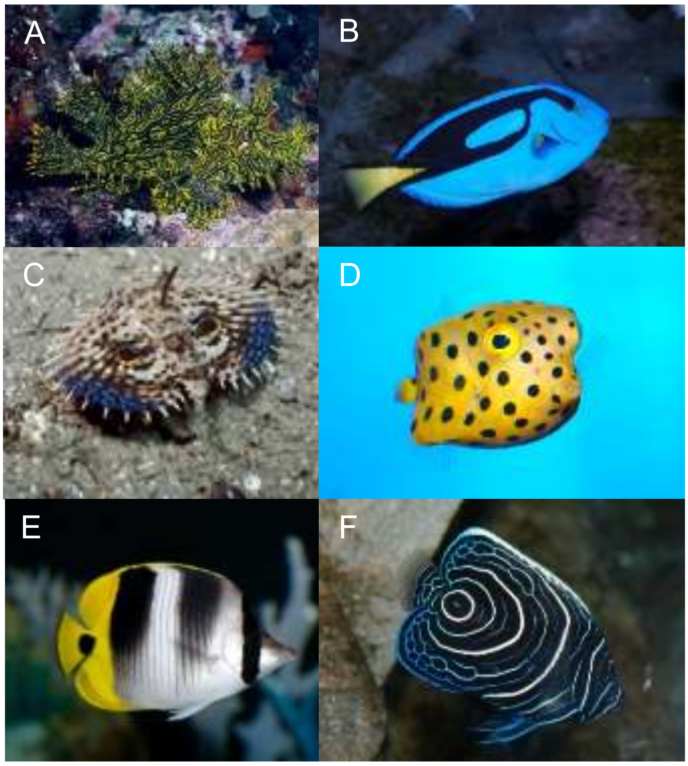

Figure 25 Lens back vertex distance as a function of beam entry position for the goldfish (*Carassius auratus*) and a suckermouth armoured catfish (*Pterygoplichthys etentaculus*).

The lenses of both the goldfish (dashed line) and the catfish(solid line) show little spherical aberration in comparison to a glass marble (dotted line). The back vertex was determined by analysing the path of a laser beam as it traversed the lens, as detailed in Douglas et al (2002). Aberration is represented by a non-linear regression fitted to the data using the following equation for back vertex distance (x); $x = a + by^2 + cy^4$, where 'a' represents back vertex focal length, 'b' the 3rd order spherical aberration, 'c' the 5th order spherical aberration, and 'y' the normalised beam entry position. Back vertex distance has been expressed relative to the maximum so that lenses with different diameters can be more easily compared. The beam entry positions have been normalised so that the edges of the lens represent 1 and –1. Curves shown are the average spherical aberration function fitted to six lenses of *C. auratus* ($x=2.10-0.52y^2+0.55y^4$) and two lenses of *P. etentaculus* ($x=2.47-0.80y^2+0.68y^4$), and a single glass marble ($x=25.91-19.03y^2-3.89y^4$) (Douglas, unpubl).

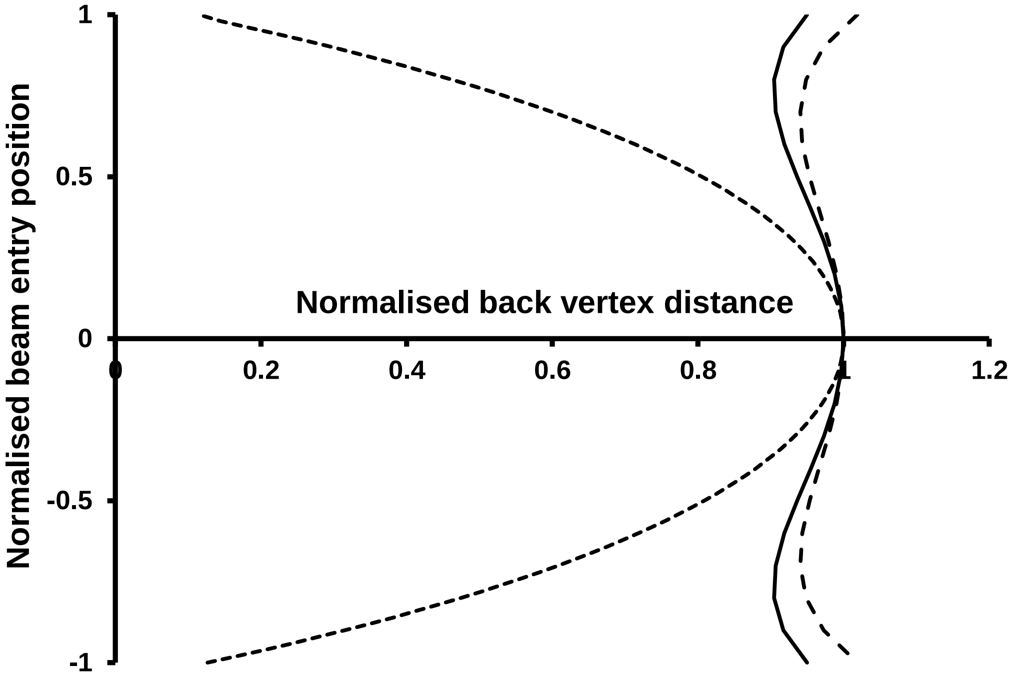

Figure 26 Effect of pupil shape on multifocal lenses.
A multifocal lens has concentric zones of differing refractive index that focus distinct wavelengths on the retina. The iris is shown by the outermost black region and the zones focussing red, green and blue light by the regions with corresponding colours. When the pupil is dilated (A) all zones of the lens are available and the entire spectrum is focused on the retina. With a constricted circular pupil (B) only blue light is focussed, while a slit pupil (C) still allows all wavelengths to be imaged on the retina (modified from Lind et al., 2008).

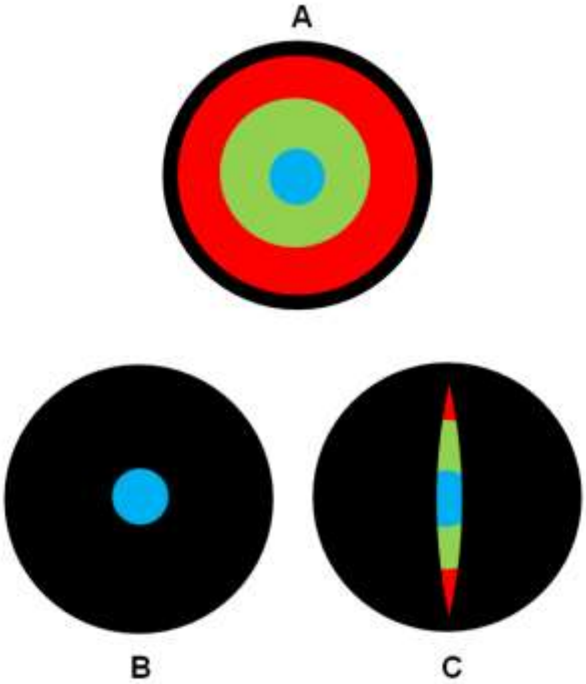

Figure 27 The eye of a yellow boxfish (*Ostracion cubicus*), showing a rostral aphakic space in the pupil (NJ Marshall).