

Colour vision in aquatic mammals—facts and open questions

Ulrike Griebel¹ and Leo Peichl²

¹Konrad Lorenz Institute for Evolution and Cognition Research, Adolf-Lorenz-Gasse 2, A-3422 Altenberg, Austria

²Max Planck Institute for Brain Research, Deutschordenstrasse 46, D-60528 Frankfurt a. M., Germany

Abstract

Aquatic mammals had to adapt to visual environments that are very different from those encountered by terrestrial mammals. Herein, we review the current knowledge on the colour-vision capabilities of aquatic mammals and discuss the puzzles that emerge from those studies. The common pattern in terrestrial mammals is dichromatic colour vision based on two spectral types of cone photoreceptors in the retina (commonly green and blue cones). Behavioural studies in a few pinnipeds and one dolphin species suggest a similar type of dichromatic colour vision in marine mammals. In contrast, recent immunocytochemical, physiological, and molecular genetic studies of the cone visual pigments in a larger sample of species show that whales and seals generally lack the blue cones and presumably are green cone monochromats. This challenges the behavioural findings, because cone monochromacy usually is tantamount to colour blindness. Furthermore, a loss of the blue cones seems a rather inadequate adaptation to the blue-dominated underwater light field in the open ocean. Other aquatic and amphibious mammals (sirenians, otters, hippopotamuses and polar bear) appear to show the more common pattern of cone dichromacy. The present review summarizes available data on the various aquatic mammalian taxa, assesses the reliability of these data, and discusses the potential adaptive pressures involved in blue cone loss. It is suggested that blue cones were lost in an early, 'coastal' period of cetacean and pinniped evolution; many coastal waters preferentially absorb blue light and constitute a long-wavelength-dominated environment. Residual colour vision in these cone monochromats could be achieved in mesopic lighting conditions by exploiting the signal differences between the remaining green cones and the rods.

Key words: Colour vision, photoreceptors, retina, eye, Pinnipedia, Cetacea, Sirenia

Introduction

The ambient light conditions in the ocean differ considerably from those on land and pose different challenges to the visual system. Marine mammals provide an excellent opportunity to study the evolutionary changes of the visual system in their re-adaptation from a terrestrial to an aquatic environment. The present review focuses on colour vision in marine mammals. Most terrestrial mammals have colour vision based on the presence of two spectral types of cone photoreceptors (commonly green-sensitive cones and blue-sensitive cones), a pattern that is termed cone dichromacy. The few behavioural studies available suggest that the same form of dichromatic—albeit poor—colour vision occurs in marine mammals. Recently, the story received an unexpected twist when immunocytochemical, physiological, and molecular genetic data demonstrated an absence of blue-sensitive cones in the eyes of whales and seals, indicating cone monochromacy and hence serious deficits in—or even the absence of—colour vision. This is at odds with the behavioural data. Furthermore, it seems strange that marine mammals should have lost the cone type that would have been most sensitive to the 'deep blue' of the open ocean. At this stage it is useful to review available data, to identify controversial and open issues, and to consider the adaptive pressures potentially involved.

Marine mammals vary in the extent of their adaptation to the aquatic environment. Cetaceans and sirenians spend all their life in water, while pinnipeds are amphibious and divide their time between land and sea. Interestingly, not only the amphibious living seals, but also the whales can see well in air. The optical and retinal structures of the eyes of marine mammals show specific adaptations for vision in both media (for a recent overview, see Supin *et al.*, 2001). The three groups of marine mammals—cetaceans, pinnipeds, and sirenians—have evolved from different terrestrial ancestors, belonging to the artiodactyls, carnivores, and

proboscideans, respectively (for recent summaries, see Gatesy & O'Leary 2001; Flynn & Nedbal, 1998; Lavergne *et al.*, 1996). We shall discuss which properties of the colour vision systems are inherited from their respective ancestors, and which properties represent convergent evolution in the environmental conditions of life in the ocean. The review also will include references to amphibious mammals adapted to freshwater habitats, such as hippopotamuses and otters.

The term 'colour vision' refers to the capability of a visual system to respond differently to light differing in wavelength only. It is based on the existence of two or more photoreceptor types containing photopigments (opsins) with different spectral sensitivity. The processing of colour-specific information in the eye and brain gives rise to the perception of colour as a subjective phenomenon. The excellent colour vision of humans is based on three spectral types of cone photoreceptors—the red, green, and blue cones—and hence the arrangement is termed trichromatic colour vision. Most mammals have less keen, dichromatic colour vision based on two cone types, one maximally sensitive in the long- or middle-wavelength range of the spectrum (L-cone, green- to red-sensitive, depending on species) and one maximally sensitive in the short-wavelength range (S-cone, blue- to ultraviolet-sensitive, depending on species; reviews: Jacobs, 1993; Ahnelt & Kolb, 2000).

Cone monochromacy, the possession of one cone type only and thus the absence of cone-based colour vision, is rare among mammals. It has been found in only a few nocturnal species, while most diurnal and nocturnal terrestrial species are dichromats (for summaries see, e.g., Jacobs, 1993; Szél *et al.*, 1996; Peichl & Moutairou, 1998; Ahnelt & Kolb, 2000). Hence, cone dichromacy is the basic mammalian pattern and also was expected in marine mammals which all have daylight activity phases and apparently use aerial vision on a regular basis. So, it came as a surprise that two groups of marine mammals, the pinnipeds and the cetaceans, have lost their S-cones and become L-cone monochromats in the evolutionary process of adapting to the marine environment (Crognale *et al.*, 1998; Fasick *et al.*, 1998; Peichl & Moutairou, 1998; Peichl *et al.*, 2001).

Colour vision requires specific neural circuits at all levels of the visual system, starting with an appropriate set of photoreceptors and perhaps not ending with colour-specific cortical neurons and areas. As Jacobs (1993) put it, 'ideally, [...] a survey of colour vision should rely on direct evidence [...], i.e. the results of appropriately conducted behavioural studies.' For practical reasons, behavioural research is often not possible and one has to rely on indirect and partial evidence. Major

sources of information are physiological and molecular studies of the visual pigments present in a given species. Formally, the presence of spectrally different visual pigments is a necessary, but not a sufficient, prerequisite for colour vision. Practically, the results of cone pigment analysis commonly agree with those of behavioural colour vision tests and hence are regarded as a robust indicator of the level of colour vision present. We shall come back to this issue later in the review. After a taxonomically organized survey of the available data, the crucial issues are discussed in more general terms across orders.

Facts

Cetacea

The cetacean eye has faced several environmental challenges in the course of evolution. It had to be re-adapted to the mechanical, chemical, osmotic, and optical conditions of the aquatic medium. There is no doubt that dolphins are highly auditory animals and toothed whales in general use echolocation extensively for orientation in their natural habitat. Nonetheless, dolphin vision serves many important biological functions, like prey detection and capture, conspecific and individual identification, and migration and orientation. A blindfolded dolphin may have difficulty finding fish at very close range even while echolocating. Also, their performance in air suggests well-developed visual function. Numerous learning experiments have demonstrated that the dolphin's visual system also supports important cognitive functions like conceptualization and communication (Herman, 1990). The structural and functional features of cetacean eyes and retinæ have most recently been summarized by Supin *et al.* (2001). One fact quite clear from the available data is that cetacean eyes, despite their large sizes compared to those of terrestrial mammals, are not designed for high acuity. The visual acuity of marine dolphins is in the range of 10 to 20 min of arc and hence is similar to or below that of many terrestrial mammals.

The cetacean eye has been modified for high light sensitivity. This is obvious from its complete retinal tapetalization, its large cornea, and its large pupillary opening that can be constricted drastically in bright light conditions above the water (Dawson, 1980). The cetacean retina contains rods and cones, but is extremely rod dominated, with cone proportions in the range of 1%. The distribution and the frequency of the receptor types varies somewhat across species and across reports from various authors (see, e.g., Pütter, 1903; Rochon-Duvigneaud, 1940; Pilleri, 1964, 1967; Pilleri & Wandeler, 1970; Perez *et al.*, 1972; Dral, 1977;

Dawson, 1980; Kastelein *et al.*, 1990; Peichl *et al.*, 2001).

The rod visual pigments (rod opsins) of whales use the chromophore retinal-1 as do those of other mammals, but their spectral tuning curves are broader than those of terrestrial mammals and are shifted to shorter wavelengths (McFarland, 1971; Fasick & Robinson, 2000; Southall *et al.*, 2002). The underwater light field becomes successively blue-shifted with depth and the positions of the rod absorption maxima (λ_{max}) indicate an adaptation to the dominant wavelengths in the environment of the species, similar to the λ_{max} ranges in many deep-sea fishes. While the rod absorption maxima in terrestrial mammals are close to 500 nm, they are 481 nm in Baird's beaked whale *Berardius bairdi*, 483 nm in the sperm whale *Physeter macrocephalus* and Cuvier's beaked whale *Ziphius cavirostris*, all deep diving species, 488 nm in the bottlenose dolphin *Tursiops truncatus*, which hunts in coastal waters, and 496 nm in the gray whale *Eschrichtius robustus*, which bottom feeds and lives in shallow neritic waters (McFarland, 1971; Fasick & Robinson, 2000; Southall *et al.*, 2002).

Recently Phyllis Robinson and her colleagues in Baltimore have cloned and expressed the opsin genes of the bottlenose dolphin, identifying the cDNAs for a rod opsin and a long-wavelength sensitive (L-)cone opsin (Fasick *et al.*, 1998; Fasick & Robinson, 1998, 2000). The resulting pigments had a λ_{max} of 488 nm for the rod and of 524 nm for the L-cone. The authors also found a gene which coded for a short-wavelength sensitive (S-)cone opsin, but it contained a deleterious mutation that prevented the expression of the S-opsin protein. Deleterious S-cone opsin genes have since been reported for further odontocete and mysticete whales (Levenson *et al.*, 2000; Robinson & Newman, 2002; D. L. Levenson, personal communication). Immunocytochemical studies using antibodies against the S-opsin also have reported a complete absence of the S-opsin in ten species of odontocetes (bottlenose dolphin, common dolphin, white-beaked dolphin, Risso's dolphin, striped dolphin, long- and short-finned pilot whale, harbour porpoise, Dall's porpoise, and northern bottlenose whale), while confirming the presence of L-cones in all these species (Peichl *et al.*, 2001; 2002). Taken together, these data suggest that toothed and baleen whales are L-cone monochromats and hence should lack the dichromatic form of colour vision typical for most terrestrial mammals.

To date, electrophysiological studies on cetacean spectral sensitivity and colour vision are non-existent and behavioural investigations are extremely rare, because animals are rarely available for such experiments and behavioural studies are very time-consuming. But, as noted in the introduc-

tion, the only way to demonstrate that an animal actually uses colour information is to perform behavioural experiments. The first behavioural study on colour vision in cetaceans was done by Madsen with a bottlenose dolphin (Madsen, 1976; Madsen & Herman, 1980). The animal had to discriminate a coloured light from a white light and also two coloured lights from each other (the stimuli were varied in intensity), first in a go/no-go discrimination task, and then in a successive two-choice discrimination task with one stimulus field and two response paddles. In both protocols, the colour stimuli were used as cues in a spatial reversal problem. Under these conditions the experimental dolphin did not demonstrate colour discrimination.

Madsen (1976) calculated the spectral sensitivity curve on the basis of a brightness match between a red, a green, and a blue monochromatic light. The dolphin's spectral sensitivity function peaked at 500 nm under photopic conditions and shifted to 496 nm under scotopic conditions. This result indicated a rod and a green cone mechanism. The scotopic shift is not very large, suggesting that the conditions might have been only mesopic for the dolphin, since the experiment was conducted under the night sky. The scotopic peak at 496 nm was 10 nm red-shifted from the λ_{max} of the extracted rod pigment of *Tursiops* (486–488 nm; McFarland, 1971; Fasick *et al.*, 1998). Similarly, the photopic peak at 500 nm was 24 nm blue-shifted from the λ_{max} of the L-cone pigment (524 nm; Fasick *et al.*, 1998). Behavioural or ERG sensitivity curves often show a shift with respect to the absorption maxima of the corresponding isolated pigments because of the spectral properties of the eye media, or incomplete dark or light adaptation (see Methodological Aspects below).

A recent behavioural study re-examined dolphin spectral sensitivity (Griebel & Schmid, 2002). In a light-adapted bottlenose dolphin, spectral sensitivity was measured in air in a spectral range from 397 nm to 636 nm in a simultaneous two-choice discrimination test by determining increment thresholds. The resulting spectral sensitivity curve was very broad, suggesting the contribution of more than one pigment and showed a sensitivity maximum in the blue-green part of the spectrum at about 490 nm. Since dolphins have lost their S-cones, the second pigment contributing to the spectral sensitivity function is probably the rod pigment. Interestingly, the curve tilted upward again in the near ultraviolet, suggesting a second maximum in the near UV. Two wavelength discrimination tasks, where brightness was adjusted to the subjective spectral sensitivity of the dolphin, showed that the dolphin could discriminate between 397 nm and 487 nm, but not between 457 nm and 544 nm. This result suggested that a mechanism for

colour discrimination is present even in the absence of S-cones.

For baleen whales, there exist no behavioural, physiological, or immunocytochemical data on colour vision capabilities, spectral sensitivity or cone opsins. The only available information is that the species studied to date have deleterious S-opsin genes and hence no functional S-cones (Levenson *et al.*, 2000). This suggests L-cone monochromacy also occurs in baleen whales.

Pinnipedia

Unlike the cetaceans and manatees, pinnipeds are amphibious and spend a substantial portion of their time on land for resting, giving birth, mating, and moulting. Like cetaceans, many pinnipeds also experience low light levels when diving or foraging at night. They did not evolve echolocation, but they possess very sensitive vibrissae which they use for turbulence tracking (Dehnhardt *et al.*, 1998; 2001). As indicated by their big eyes, vision plays a significant role in pinnipeds for various biological functions like hunting, orientation, and communication. As members of the carnivore order, pinnipeds have rather frontally positioned eyes and an extended binocular field-of-view that suggests good depth perception. The structural and functional features of pinniped eyes and retinae have most recently been summarized by Supin *et al.* (2001). Visual acuities of seals and sea lions are in the range of a few minutes of arc. This reasonably good acuity is similar to that of terrestrial carnivores, e.g. dogs and cats.

In adaptation to low-light conditions, the eyes of pinnipeds have well-developed tapeta behind most of the retinal area (Bräckevelt, 1986). Their retinae are densely populated with highly light-sensitive rods, but also contain sparse populations of cones, constituting about 1% of the photoreceptors (Landau & Dawson, 1970; Jamieson & Fisher, 1971; Nagy & Ronald, 1975; Mass, 1992; Peichl & Moutairou, 1998; Peichl *et al.*, 2001, 2002). Behavioural evidence also suggested a duplex retina featuring a Purkinje shift, a break in the dark adaption curve (Lavigne & Ronald, 1972; Levenson & Schusterman, 1998) and a break in the critical flicker-frequency curve (Bernholz & Matthews, 1975).

The spectral absorption curves of pinniped rod visual pigments are shifted to shorter wavelengths than those of terrestrial mammals, with a λ_{max} at about 496 nm in the shallow diving California sea lion *Zalophus californianus* and harbour seal *Phoca vitulina*, and a λ_{max} of 483 nm in the deep diving northern elephant seal *Mirounga angustirostris* (Lythgoe & Dartnall, 1970; Lavigne & Ronald, 1975; Lavigne *et al.*, 1977; Fasick & Robinson, 2000; Southall *et al.*, 2002). Furthermore, the rod

system in the last-mentioned species seems to be able to adapt extremely fast, attaining its threshold sensitivity within 6 min (Levenson & Schusterman, 1999). So, pinniped rod pigments, like those of cetaceans, appear to be adapted to diving depth.

The behaviourally measured photopic spectral sensitivity of the harp seal showed a main maximum at 550 nm and a secondary peak near 480 nm (Lavigne & Ronald, 1972). A behavioural study of photopic spectral sensitivity in the harbour seal and southern sea lion (*Otaria byronia*) yielded similar results (peak sensitivities around 500 nm and around 540 nm, respectively: Griebel, König & Schmid, submitted). In both studies, the main peak indicating an L-cone was very broad, suggesting the contribution of a second pigment type (probably the rod pigment). The secondary, short-wave peak in all these behavioural curves suggested the presence of a second, short-wave sensitive (blue) cone.

The sensitivity picture has been corroborated by behavioural studies on colour discrimination. The first psychophysical investigation of colour discrimination was performed with a spotted seal, *Phoca largha* (Wartzok & McCormick, 1978). The results suggested that this species has some kind of colour vision since the animal discriminated between blue and orange targets. A more detailed investigation with two species of fur seals, *Arctocephalus pusillus* and *A. australis*, showed that the animals were able to distinguish blue and green from grey, but failed to discriminate red and yellow from grey (Busch & Duecker, 1987). Another behavioural study using similar methods with California sea lions reported the same results (Griebel & Schmid, 1992).

In contrast, a study using flicker-photometric electroretinography (ERG) indicated that harbour seals possess a photopic λ_{max} of 510 nm and showed by a test for univariance that this species has only one cone type, the L-cone (Crognale *et al.*, 1998). Immunocytochemical studies with antibodies against the opsins of L- and S-cones in eight species of phocids and otariids also demonstrated a complete absence of S-cones in all these species, while L-cones were present at the expected low densities [species studied: ringed seal (*Phoca hispida*), harbour seal, grey seal (*Halichoerus grypus*), hooded seal (*Cystophora cristata*), bearded seal (*Erignathus barbatus*), Australian fur seal, northern fur seal, and southern sea lion; Peichl & Moutairou, 1998; Peichl *et al.*, 2001; 2002]. Interestingly, the genetic basis for the S-opsin loss appears to differ among seal species. The harp seal (*Phoca groenlandicus*)—like the cetaceans referred to above—has a defective S-opsin gene, whereas the harbour seal has an intact S-opsin gene, but no retinal S-opsin mRNA, suggesting deleterious mutations at the promoter or splice site level (Robinson & Newman, 2002).

The conclusion from the physiological, cellular, and genetic evidence is that, like the cetaceans, the pinnipeds have lost their S-cones and only retained the L-cones. Since colour vision in mammals is typically cone-based and involves the comparison of signals from two or more cone types, in pinnipeds this form of colour vision should not exist. That is surprising in a group spending a large proportion of time on land or in shallow waters, where the light is spectrally broad and would allow colour vision.

Sirenia

Sirenians, which include manatees, dugongs and the extinct Steller's sea cow, are aquatic herbivorous mammals which inhabit the rivers and coastal zones of the tropical seas. They have nocturnal and diurnal activity phases. Little is known about the sensory apparatus or capabilities of sirenians. Questions regarding their orientation, navigation, vision, taste, and tactile senses have just begun to be explored. The available data have been summarized recently by Supin *et al.* (2001). While most of the early investigators considered sirenian vision to be very poor, a more favourable view now has emerged from observations of visually guided behaviour in the Florida manatee *Trichechus manatus* (Hartman, 1979; Gerstein, 1994; Griebel & Schmid, 1996). Although there are earlier contradictory reports about the presence of a tapetum in the sirenians, there seems to be no tapetum lucidum in the manatee eye (Piggins *et al.*, 1983; P. Ahnelt, personal communication).

A light and electron microscopic study of the *Trichechus manatus* retina revealed both rod-like and cone-like photoreceptors (Cohen *et al.*, 1982). The average cone-to-rod ratio reported was 1:2.4, indicating a much greater importance of cone-based vision than in cetaceans and pinnipeds. Actually, the cone proportion of some 30% appears improbably high for an arrhythmic mammal, because even most diurnal species have only 5–15% cones. Further investigation is needed in this case. Preliminary immunocytochemical data indicate the presence of both L-cones and S-cones in the manatee retina (Ahnelt & Bauer, personal communication). Recently, a genetic analysis of the manatee has established the presence of intact S-opsin and L-opsin genes, which are expressed in the retina (Robinson & Newman, 2002). All this argues for the presence of cone-based dichromatic colour vision.

The rod visual pigment has been analyzed in the Amazon manatee *Trichechus inunguis* (Piggins *et al.*, 1983). The extracted rod visual pigment is based on retinal-1 and has a λ_{\max} of about 505 nm. Given that many terrestrial mammals have a rod pigment λ_{\max} close to 500 nm, the manatee's

freshwater environment has probably resulted in a slight red-shift of its rod pigment.

At present, there is only one behavioural study exploring the capabilities for colour vision in this group (Griebel & Schmid, 1996). Four *Trichechus manatus* individuals were trained to discriminate between a coloured stimulus and a shade of grey in a two-fold simultaneous choice situation. The colours blue, green, red, and blue-green were tested against shades of grey varying from low to high relative brightness. The animals distinguished both blue and green from a series of greys, but failed to discriminate a specific hue of blue-green from certain steps of greys, suggesting a neutral point typical for cone dichromats. The colours blue, green, and red also could be distinguished from each other. These results suggest conventional dichromatic colour vision. The manatees could not discriminate between a UV-reflecting white target and an UV-absorbing white target. In summary, all available evidence indicates that, in contrast to cetaceans and pinnipeds, manatees have preserved the two spectral classes of cones. We are not aware of any data on the cone types and colour vision of dugongs, the other extant sirenian clade.

Other amphibious mammals

When searching for the environmental pressures that led to a loss of the blue cones in cetaceans and pinnipeds, but not in sirenians, it is instructive to look at other mammals that have partly adapted to freshwater or seawater, i.e. amphibious mammalian species. Most prominent among them are the artiodactyl hippopotamuses, and two carnivore groups, the otters and polar bears. Because the pinnipeds are carnivores and the cetaceans are closely related to the artiodactyls, one can assume common ancestral photoreceptor equipments and hence, confidently attribute observed differences to different adaptive pressures.

Otters—The amphibious otters (mustelid carnivores) live in rivers, lakes, or close to the sea shore. Unlike the river otters (*Lutra spp.*), the sea otter (*Enhydra lutris*) rarely ever leaves the water and stays most of its life close to the sea shore, seeking protection in kelp beds. River otters are active during both day and night and feed mostly on fish. Behavioural observations (Erlinge, 1968) and experiments (Green, 1977) have shown that the river otter hunts predominantly by vision. Green (1977) showed that the otter takes four times longer to find prey in turbid water than in clear water. Without vibrissae the time necessary to find the prey stays the same in clear water, but takes 20 times longer in turbid water.

River otters (*Lutra lutra*) possess an extensive tapetum lucidum cellulare and the retina contains

rods and cones (Pilleri, 1967). There are S-cones as well as L-cones in low densities, thus showing the typical mammalian dichromatic pattern (Peichl *et al.*, 2001). Behavioural experiments with *L. lutra*, carried-out in shallow water, have shown that it can discriminate the colours blue and green from various shades of grey (Kasprzyk, 1990). The Southeast Asian river otter (*Amblonyx cineria cineria*) was able to discriminate red and green from greys (Balliet, 1970). In the sea otter, Mass & Supin (2000) have analyzed the retinal ganglion cell distribution and derived a retinal resolution (visual acuity) of about 7 min of arc in water. We are not aware of any colour vision studies in sea otters.

Polar bear—The preferred habitat of polar bears (*Thalarctos maritimus*, an ursid carnivore) is the pack ice, so much so that it has resulted in a white fur as an adaptive coloration. The polar bear's preferred food is ringed seal, which it commonly hunts on ice or at the water's edge. Polar bears are good swimmers and in water also feed on sea birds and fish. Hence, they can be considered well-adapted to marine life. Polar bears are active under various illuminations from bright sunshine on snow to mid-winter darkness, but there is little information on their visual abilities and on the extent to which they depend on sight (for references, see Ronald & Lee, 1981). The visual environment of the pack ice zone is dominated by shades of white and grey and offers hardly any opportunity for colour vision.

Nevertheless, the only available study on polar bear spectral sensitivity, which is a behavioural one, reports a bimodal photopic curve with peaks at 525 nm and 450 nm, suggesting the presence of L-cones and S-cones (Ronald & Lee, 1981). The scotopic sensitivity peaks at 525 nm, suggesting a red-shifted rod pigment. So, we assume that the polar bear is a normal cone dichromat, while further studies are necessary to firmly establish the existence and extent of its colour vision capabilities.

Hippopotamus—Very little is known about the visual system of the hippopotamus (*Hippopotamus amphibius*), an African amphibious freshwater mammal that spends most of its time in rivers and lakes and only leaves the water during the night for grazing. Luck (1965) described cones in the hippopotamus retina. An immunocytochemical assessment of the cone opsins in the pygmy hippopotamus (*Choreopsis liberiensis*) has demonstrated the presence of S-cones and L-cones (Peichl *et al.*, 2001). This suggests normal dichromatic colour vision, but to date no behavioural experiments have been done.

Discussion

Two puzzles

Regarding whales and seals, two obvious puzzles emerge from the above survey. First, there is the apparent contradiction between the photoreceptor data indicating cone monochromacy, and the behavioural data indicating some capacity for colour vision. Here, one has to critically examine the reliability of various data and to consider whether colour vision is at all possible with just one cone type. The second puzzle is the loss of the blue-sensitive cone type in an environment that is dominated by blue light, i.e. the sacrifice of a seemingly fitting photoreceptor. What are the actual viewing conditions in different waters, what is potentially gained by the blue cone loss, and what are the evolutionary paths involved? These are the issues for the remaining sections of this review.

Methodological aspects

Immunocytochemistry, genetics, physiology—The evidence for the absence of S-cone opsin in whales and seals is convincing. The most convenient method to identify cone opsins across a large number of species has been immunocytochemical labelling of the L- and S-cones with opsin-specific antibodies. As discussed in Peichl *et al.* (2001), the antibodies used in these studies have proven to reliably label the respective opsins in a wide range of species across mammalian orders, specifically in terrestrial species that are closely related to the whales and pinnipeds. One might argue that the S-opsins of marine mammals are molecularly modified to an extent that prevents recognition by the antibodies. However, given the reliability of the labelling across distant mammalian taxa, this seems unlikely. For the ringed seal, it has been shown directly that all cones contain the L-opsin, i.e. there are no cones with an unidentified opsin (Peichl & Moutairou, 1998). Another concern is poor tissue preservation, since specimens from stranded animals often have been fixed relatively late *post mortem* and stored in a fixative for extended periods. So, photoreceptor outer segments could have been damaged or opsins decomposed. However, the presence of L-opsin immunoreactivity in the same tissue and the successful labelling of S-opsin in terrestrial mammalian tissue that had been similarly treated, argues against tissue preservation being a critical factor.

Support for the immunocytochemical data comes from genetic studies performed in some species (Fasick *et al.*, 1998; Fasick & Robinson, 1998; Levenson *et al.*, 2000; Robinson & Newman, 2002). They showed that S-opsin genes are present in all the seals and whales studied, but that these genes

contain deleterious mutations preventing expression of the opsin protein. This provides a proximal explanation for the lack of S-cones. It also indicates that the ancestors of whales and seals once possessed S-cones.

One property of the available opsin antibodies is that they label any member of the S-opsin or L-opsin family, irrespective of the exact spectral sensitivity of the visual pigment. Generally, this is advantageous because the labelling is not subject to species-specific spectral shifts. The S-opsin antibodies label the blue-sensitive S-cones of carnivores and ungulates, as well as the UV-sensitive S-cones present in some rodents. The L-opsin antiserum labels green-sensitive, as well as red-sensitive L-cones. But, there is a shortcoming. If whales or seals had more than one spectral opsin type belonging to the L-opsin family, the L-opsin antiserum would label them indiscriminately. So, one might argue that whales and seals could have two L-cone types and thus, dichromatic colour vision despite the absence of S-cones. However, this possibility is ruled-out by the genetic data showing only one L-opsin gene product. Furthermore, an ERG study in the harbor seal demonstrated that its photopic spectral sensitivity curve is best fitted by a single (green) cone opsin absorption curve (Cognale *et al.*, 1998). It also should be noted that L-opsin polymorphism has not been reported in any mammal outside primates.

Taken together, the cellular data provide sound evidence for an S-cone loss in a substantial number of whales and seals. Even though the sample of species is small (e.g. baleen whales are distinctly under-represented), it is broad enough to put forward the working hypothesis that cetaceans and pinnipeds have generally lost their S-cones and are L-cone monochromats.

Behaviour—Two types of behavioural experiments on colour vision have been performed. One involves a colour discrimination task where the animal is trained to discriminate various coloured stimuli from grey stimuli or other colour stimuli in a forced-choice situation. Different shades of grey from low to high relative brightness, and/or colour stimuli varying in brightness, are tested against each colour to rule-out the possibility that the animal uses brightness cues to succeed in the task. The second is a measurement of the spectral sensitivity function, where the animal is trained to respond to faint monochromatic light stimuli across the visible spectrum. The detection threshold for stimulus intensity at each wavelength is determined to obtain the spectral sensitivity curve. Both methods can be performed at photopic and scotopic ambient light levels to obtain cone- and rod-based performance, respectively. The first method directly tests the

ability to discriminate colours. The second only measures the sensitivity to various wavelengths, giving information on the spectral characteristics of the photoreceptors and visual pigments involved, but this method cannot determine whether the animal uses these signals for colour vision.

Behavioural colour vision experiments are notoriously difficult and conditions are less stringently controllable than in cellular studies. First, the animal has to cooperate, i.e. it has to respond to a stimulus it perceives. The variability across individuals reported in many of the marine mammal studies shows that this problem is not negligible. However, while a negative result could merely indicate that the animal has not 'understood' or 'attended to' the task, a positive result is more reliable. Second, one has to rule-out the possibility that the animal uses brightness cues instead of colour cues to discriminate stimuli. The perception of relative brightness varies across species, so as a starting point one has to assess the appropriate stimulus parameters for each species. Our knowledge of these parameters has continuously increased, such that recent studies are commonly better controlled and hence more reliable than the older studies. Third, photopic and scotopic conditions have to be defined for each species to obtain pure cone- or rod-driven responses. Mesopic conditions, intermediate between scotopic and photopic light levels, are those where both rods and cones are in their working range. Depending on pupillary mechanisms, the optical properties of the eye media, the presence of a reflecting tapetum, etc., an illumination level that is scotopic for a human observer could be mesopic for another species, and *vice versa* a human photopic level could be mesopic for some other species. As we shall see below, an interaction between rods and cones can provide some colour vision even in cone monochromats. Many behavioural studies on marine mammal colour vision have assumed photopic or scotopic conditions without being able to prove that they were operative during the tests.

A further difficulty is found in correlating the maxima of behavioural spectral sensitivity curves with the spectral absorption maxima of isolated visual pigments. The spectral transmission properties of the eye media, the interaction of rods and cones at mesopic light levels, the processing characteristics of postsynaptic retinal neurons, and further factors often result in shifts of behaviourally determined sensitivity maxima with respect to those of the underlying visual pigments. It is sometimes plainly impossible to reconcile the two sets of data. The harp seal could serve as an example in case. Its behavioural photopic and scotopic sensitivity functions were measured by Lavigne & Ronald (1972). The photopic curve has two maxima near 550 nm

(yellow-green) and 480 nm (blue). Does this indicate two cone types, one green-sensitive and one blue-sensitive? Recent evidence showed that the harp seal has no blue cones (Robinson & Newman, 2002; Peichl, unpublished observations). The behavioural scotopic curve has a maximum near 520 nm, with a secondary bulge at 450 nm (Lavigne & Ronald, 1972). But, the rod opsin of the harp seal has a λ_{max} of 497 nm (Lavigne & Ronald, 1975). Could the testing conditions have actually been mesopic, such that both the 'photopic' and the 'scotopic' curve contain cone and rod contributions? In the photopic curve, a 497 nm rod would not explain the 480 nm secondary maximum. In the scotopic curve, an L-cone contribution might explain the long-wave shift from 497 nm to 520 nm, but there is no S-cone to explain the 450 nm bulge. Hence, the blue sensitivity in the behavioural curves remains a puzzle.

Can cone monochromats see colour?

The ability to discriminate colours requires the existence of two or more spectral photoreceptor types. As a rule these are the cones, because for physical and biochemical reasons colour vision requires a certain amount of light intensity, i.e., a substantial photon flux onto the photoreceptors, to increase the signal-to-noise ratio. Colour vision is most acute in photopic conditions, when input into the visual system comes exclusively via the cones. But, colour vision (somewhat reduced) also is possible in mesopic conditions, when the cone signals are less strong. This is the light level where the working ranges of cones and rods overlap, and where rod signals, which are spectrally different from those of the cone(s), might be included in neural computations to extract colour information.

In fact, rod contributions to colour vision have been demonstrated. The owl monkey (*Aotus trivirgatus*), one of the few terrestrial L-cone monochromats, has residual colour vision under mesopic conditions and this has been attributed to the interaction of the rods and the persisting L-cones (Jacobs *et al.*, 1993). Human S-cone monochromats—people with a rare genetic disorder who have no red and green cones, just blue cones and rods—can distinguish wavelengths in the range of 440 to 500 nm with near-normal precision, provided the ambient illumination is mesopic (Reitner *et al.*, 1991). Beyond 500 nm, wavelength discrimination deteriorates rapidly, and in photopic conditions wavelength discrimination breaks down completely. This indicates that the discrimination is made by using S-cone and rod signals, which is not possible at photopic light levels. The human rod has a λ_{max} of about 500 nm and the S-cone of about 420 nm, explaining the good wavelength

discrimination in the 440 to 500 nm range and its failure at longer wavelengths.

Hence, in principle, colour vision is possible for cone monochromats. But, it is restricted to mesopic lighting conditions where the rods can contribute and it appears to be spectrally limited by the absorption curves of the rod opsin and the available cone opsin. For marine mammals with a rod λ_{max} between 481 and 500 nm and an L-cone λ_{max} between 510 and 525 nm (depending on species, see above), one would predict colour discrimination in the rather narrow wavelength range of about 480 to 520 nm (blue-green part of the spectrum) and a failure to discriminate shorter or longer wavelengths. This prediction is compatible with the behavioural findings that fur seals and the California sea lion can discriminate blue and green from grey, but not red and yellow from grey (Busch & Duecker, 1987; Griebel & Schmid, 1992).

We also reason that the behavioural studies reporting colour vision in seals and whales must in fact have been conducted at mesopic light levels, even when photopic conditions were assumed by the investigators. Mesopic, rod-cone colour discrimination offers the most parsimonious explanation to reconcile the behavioural results with the demonstration of L-cone monochromacy, as has been suggested by Crognale *et al.* (1998).

Vision in the marine environment

In trying to understand why cetaceans and pinnipeds, but not other aquatic and amphibious mammals, have lost their short-wave sensitive cones and thus jeopardized colour vision, we look to the specific conditions of vision in aquatic environments. The traditionally claimed advantage of colour vision is that it promotes the perception of contrast, thus enhancing the visibility of an object in a complex surrounding. Another advantage is colour constancy. Objects in the visual environment are typically illuminated by some combination of direct and indirect lighting and this can lead to significant local and temporal variations in brightness and shadowing. Variations in brightness may be substantial, whereas the variations in colour are considerably smaller. Therefore, the discrimination of objects will be more reliable if the observer uses colour cues. Also, the 'signal significance' of colours plays an important role and allows the observer to discern something about the nature of an object.

In the aquatic environment, the photic conditions differ in many respects from those in air. One aspect is image quality. Suspended particles and water molecules scatter light in all directions. These scattering effects, much more pronounced in water than in air, lead to a strong decrease of contrast and acuity with increasing distance (Jagger & Muntz, 1993). Another aspect is the intensity and spectral

composition of the available light. Some light intensity is lost by reflection of incident light at the water surface, and the scattering and absorption of light in the water drastically reduce brightness with depth. Depending to the type of water and the suspended and dissolved material, different wavelengths are very differently scattered and absorbed. In the clear water of the open ocean, blue light (450–480 nm) penetrates deepest; in eutrophic waters, turbidity leads to a shift towards the red part (around 600 nm) of the spectrum (Jerlov, 1976; Kirk, 1994).

Thus, relative darkness, a narrow spectrum, reduced contrast, and short-range visibility are characteristics of the deeper aquatic environment. As whales and seals make most of their living under water and are also arrhythmic, i.e. active during the day as well as during the night, they should have special adaptations for relative darkness under water. Examples for such adaptations are strong rod dominance and the presence of reflecting tapeta in all whales and pinnipeds and unusually rapid dark adaptation in deep-diving pinnipeds (Levenson & Schusterman, 1999). One can conclude that the dominant pressure on the visual systems of whales and seals was for optimizing scotopic, rod-mediated vision.

Nevertheless, whales and pinnipeds have retained a small population of cones to cope with higher light intensities, as have all nocturnal terrestrial mammals, which are similarly adapted to scotopic vision. The stunning difference is that most nocturnal terrestrial mammals have L-cones and S-cones and hence, the potential for dichromatic colour vision, whereas all whales and seals studied to date are L-cone monochromats. If this difference is due to the aquatic environment, it appears paradoxical. Even if colour vision is not an issue in a relatively monochrome blue underwater environment, the S-cones would be better suited than the L-cones to detect intensity and contrast cues. Matched pigments are postulated by the 'sensitivity hypothesis' of F. W. Munz, implying that for optimal sensitivity visual pigments should be tuned to the available wavelengths (review: Lythgoe & Partridge, 1991). This is emphasized by the fact that the spectral sensitivities of the rods and L-cones of many marine mammals are somewhat blue-shifted from those of terrestrial mammals, suggesting an adaptive move towards the available wavelengths. The broad spectral absorption curves of the L-opsins actually extend into the blue part of the spectrum, albeit with reduced sensitivity. So why have the S-cones and not the L-cones been lost?

Some hypotheses

Offset pigments—One explanation for a spectral mismatch between visual pigments and the under-

water lightfield was proposed by Lythgoe (review: Lythgoe & Partridge, 1991). This 'contrast hypothesis' implies that 'offset' pigments with longer-wavelength sensitivity than that of the blue ambient light would improve the detection of contrast between an object and the background—provided that the object's reflection is spectrally broader than the background light. However, this condition only holds for reflective objects (e.g., fish) viewed horizontally at short ranges in shallow water, where the downwelling light reflected by the object has a shorter path length in water to the observer's eye and hence is spectrally broader than the background light and the veiling light that travels a longer distance through the water's blue spectral filter. In all other cases—objects darker than the background, and both bright and dark objects in deep water or at longer distances or seen from below—the advantage of offset pigments disappears and matched pigments are more efficient. Lythgoe & Partridge (1991) concluded that retinæ containing matched as well as offset pigments would be optimally equipped for all potential underwater viewing conditions. Clearly, this is not the case in whales and pinnipeds.

Chromatic aberration—Another line of argument considers optical reasons for L-cone monochromacy. Highly light-sensitive eyes require an aperture (pupil) that is large in relation to the focal length of the eye. This leads to a very short depth of focus, often much shorter than the differences in focal length for the different wavelengths (termed longitudinal-chromatic aberration), and only a narrow band of wavelengths can be simultaneously in focus on the retina. A number of fishes and terrestrial vertebrates have solved this problem of chromatic defocus with multifocal lenses. Each focal length of the lens creates a sharp image for one of the spectral cone types (Kröger *et al.*, 1999; Kröger, 2000). However, such a mechanism sacrifices sensitivity and contrast for improved colour detection. Maximal light gathering can only be achieved with monofocal lenses. With these, all photoreceptors should have similar spectral sensitivities, because other wavelengths are out of focus. As the λ_{max} of the rods, which are the crucial photoreceptor type in highly sensitive eyes, is closer to the λ_{max} of the L-cones than to that of the S-cones, the latter could have been lost because there was no useful image in their spectral sensitivity range. The properties of marine mammal lenses have yet to be determined to test this hypothesis. Also, it is unclear why nocturnal terrestrial mammals, which are faced with the same demands on light sensitivity, have not taken the same path, but instead have retained both cone types.

Tapetum lucidum—The tapetum lucidum, a reflective layer behind the retina, greatly increases light capture by the retina but it also acts as a spectral filter, evidenced by its colour when observed in white light. Both the pinnipeds and the whales have tapeta like their terrestrial relatives, the carnivores and artiodactyls. Could the spectral narrowing of the available light by the tapetum have led to the loss of the S-cones? The cat's tapetum, which is green or yellow (depending on the individual), has a high spectral reflectance in the 500–600 nm range and a steeper decrease towards the blue than the red end of the spectrum. Nevertheless, the spectral sensitivity of the cat's retina, measured by ERG, shows no difference between tapetal and non-tapetal regions (cat data reviewed in Muntz, 1972); and, the cat has L- and S-cones. Hence, the tapetum does not exert a significant influence on spectral sensitivity or cone types. The tapeta of artiodactyls (also possessing L- and S-cones) have individually varying green, yellow, and sometimes blue regions.

In odontocetes, the tapetal colours of fixed eyes were reported to differ among species, individuals and fundus regions, covering the range from yellow to green to blue to whiteish (Pütter, 1903; Dawson, 1980). Some of this range can be attributed to fixation-induced changes. The *in vivo* colouration of the tapetum has been assessed in *Tursiops truncatus* and *Grampus griseus* (Dawson *et al.*, 1987). Here, *Tursiops* has a green-yellow tapetum with little inter-individual variation; the tapetum of *Grampus* has a more blue-shifted appearance. The study also gives spectral measurements, indicating high reflectance in the 500–700 nm range and low reflectance below 500 nm in *Tursiops*, and high reflectance for 450–700 nm light in *Grampus*. Qualitatively, this is not too different from the situation in the cat.

Most (fixed) pinniped tapeta seem to be dull blue-grey, while metallic yellow in the genus *Phoca* (Pütter, 1903). Hence, depending on species, the tapeta of whales and seals are similar to or blue-shifted from those of terrestrial mammals, perhaps indicating some adaptation to the underwater environment. Extrapolating from the cat findings above, one can assume that such tapeta would not put the blue cones at a disadvantage and thus cannot explain the S-cone loss.

S-Cone loss an ancient adaptation?

The above hypotheses are worth following up, but at present they do not give satisfactory explanations for the S-cone loss. One reason is that the loss occurs in shallow and deep divers, in coastal and in open sea dwellers, in the purely aquatic whales and the amphibious pinnipeds, i.e., in species that are exposed to rather different photic environments. Should that not have imposed different adaptive pressures, favouring an S-cone loss in some species,

but not in others? To overcome this dilemma, we have hypothesized that the S-cone loss may not be related to adaptive pressures in the present habitats, but may have occurred rather early in the evolution of whales and pinnipeds in adaptation to a different, more uniform photic environment (Peichl *et al.*, 2001).

The basic mammalian pattern is cone dichromacy. In particular, modern terrestrial artiodactyls and carnivores are conventional dichromats with L-cones and S-cones (comparative overviews: Jacobs, 1993; Szél *et al.*, 1996; Ahnelt & Kolb, 2000). Thus, it can be assumed that the terrestrial ancestors of whales and pinnipeds had S-cones. This is supported by the persisting presence of the S-opsin genes, *albeit* defective. The parallel loss of the S-cones in the marine members of two distinct orders, but not in their terrestrial close relatives, argues for convergent evolution and an adaptive pressure exerted by the marine habitat. The absence of S-cones in all pinnipeds and all cetaceans studied to date suggests an early occurrence of the genetic change, which then spread throughout their respective radiations. So, the most likely time was shortly after the return of ancestral whales and seals to the sea. During this initial, partly amphibious phase, they are thought to have inhabited coastal waters (Gingerich *et al.*, 1983).

In many coastal marine waters, the underwater light spectrum is red-shifted due to blue light absorption by organic and inorganic material from land drainage and biological debris (gilvins, 'Gelbstoffe'); even at relatively shallow depths and photopic light levels, there is little blue light remaining (Dartnall, 1975; Jerlov, 1976; Loew & McFarland, 1990). In such conditions, a loss of the 'jobless' blue cones may not have constituted a significant disadvantage and could even have been an economical adaptation, simplifying retinal and cortical visual information processing. Some descendant species have stayed in coastal waters and for these the S-opsin loss remains useful or at least neutral. Other descendant species have later conquered the open ocean in adaptive evolutionary radiation. They might now have profited from a functional S-opsin, but they could not reverse the deleterious gene defect. All they could apparently do was shift the spectral tuning of their remaining photoreceptors to shorter wavelengths.

Assuming a loss of the S-cones shortly after the emergence of cetaceans and pinnipeds, respectively, we originally thought that the underlying genetic change should be rather similar (homolog) within each order while differing between the orders (Peichl *et al.*, 2001). However, recent preliminary evidence suggests different genetic loci of the defect in two phocids (Robinson & Newman, 2002) and some whales (D. H. Levenson, personal

communication). One might conclude that within each order the S-cone loss occurred independently several times. Another, more parsimonious interpretation is that within each order a common, as yet unidentified genetic change, e.g., in the promoter of the S-opsin gene, exists in all species, thwarting the expression of an S-opsin protein and hence allowing secondary, species-specific mutations to accumulate in the gene itself (L. Newman & P. Robinson, personal communication). Further data are necessary to test these hypotheses and to decide between the 'one event' and the 'multiple independent events' scenarios. It also could be possible to identify the time point(s) of S-cone loss and to check for coincidence with the early 'coastal' period. While multiple, independent losses of S-cones would emphasize the power of the adaptive pressures involved, they also leave open the possibility that some cetacean or pinniped may yet be found to have kept its S-cones.

The manatees, which live in a coastal habitat, seem to have retained cone dichromacy and the ability to discriminate colours. There could be two reasons for this: (1) They live in very shallow estuaries, swamps and rivers where the available light is bright and probably spectrally broader than the coastal marine habitat encountered by the early whales and pinnipeds. (2) They are herbivores that need to discriminate fresh plants from rotten ones and from other objects, favouring the conservation of adequate colour vision (Ahnelt & Kolb, 2000).

The freshwater habitats of the amphibious river otter and hippopotamus also are shallow compared to the coastal marine habitats encountered by early whales and seals, suggesting a spectrally broader photic environment. Furthermore, their considerable terrestrial activities in a vegetated, spectrally richer environment could have helped to conserve cone dichromacy and colour vision. In comparison, the sandy or rocky terrain normally encountered by pinnipeds during their terrestrial activities is drab.

Finally, there is an interesting parallel to fish (see, e.g. Partridge, 1990). Many surface-living diurnal species of fish have several spectral cone types and good colour vision—comparing well with the situation in manatee, river otter and hippopotamus. Deeper living, but still diurnal, freshwater fishes possess red cones and commonly have abandoned the S-cones, presumably as an adaptation to their spectral environment, as deeper freshwater, like coastal marine water, is dominated by long-wave light. This compares nicely with the situation postulated for early whales and pinnipeds. The similarity vanishes for deeper living and crepuscular marine fishes, which usually possess blue and green cones, interpreted as an adaptation to the blue-shifted lighting conditions of deeper waters. The pattern in fishes again emphasizes the puzzle of the

blue cone loss in cetaceans and pinnipeds and argues for their adaptation to an early, coastal photic environment.

Outlook

The issue of colour vision in marine mammals remains a challenge for marine biologists and neuroscientists. More species, particularly baleen whales, river dolphins, and the walrus have to be studied to check the hypothesis that all whales and pinnipeds have lost their S-cones. Further behavioural experiments have to scrutinize the extent to which whales and pinnipeds are able to discriminate colours, to precisely define the photic conditions (mesopic or photopic) in which they can do so, and to establish the role of rods in this performance. Further molecular analyses need to show how different the deleterious mutations in the S-opsin genes actually are across species, and whether or not there is a common basic defect in the S-opsin gene control region. Molecular genetics may also clarify at what time points in cetacean and pinniped evolution the S-cones were lost.

Literature Cited

- Ahnelt, P. K. & Kolb, H. (2000) The mammalian photoreceptor mosaic—adaptive design. *Progress in Retinal and Eye Research* **19**, 711–777.
- Balliet, R. F. (1970) Color discrimination in the Southeast Asian river otter (*Amblonyx cineria cineria*). *Master's Thesis*, San Francisco State College, California.
- Bernholz, C. D. & Matthews, M. L. (1975) Critical flicker frequency in a harp seal: evidence for duplex retinal organization. *Vision Research* **15**, 733–736.
- Braekveelt, C. R. (1986) Fine structure of the tapetum cellulosum of the grey seal (*Halichoerus grypus*). *Acta Anatomica* **127**, 81–87.
- Busch, H. & Duecker, G. (1987) Das visuelle Leistungsvermögen der Seebären (*Arctocephalus pusillus* und *Arctocephalus australis*). *Zoologischer Anzeiger* **219**, 197–224.
- Cohen, J. L., Tucker, G. S. & Odell, D. K. (1982) The photoreceptors of the West Indian manatee. *Journal of Morphology* **173**, 197–202.
- Crognale, M. A., Levenson, D., Ponganis, P. J., Deegan, J. F., & Jacobs, G. H. (1998) Cone spectral sensitivity in the harbor seal (*Phoca vitulina*) and implications for color vision. *Can. J. Zool.* **76**, 2114–2118.
- Dartnall, J. H. A. (1975) Assessing the fitness of visual pigments for their photic environments. In: M. A. Ali (ed.) *Vision in Fishes: New Approaches in Research*, pp. 543–563. Plenum Press, New York.
- Dawson, W. W. A. (1980) The cetacean eye. In: *Cetacean Behavior* L. M. Herman (ed.), pp. 53–100. Wiley, New York.
- Dawson, W. W., Schroeder, J. P. & Dawson, J. F. (1987) The ocular fundus of two cetaceans. *Marine Mammal Science* **3**, 1–13.
- Dehnhardt, G., Mauck, B. & Bleckmann, H. (1998) Seal whiskers detect water movements. *Nature* **394**, 235–236.

- Dehnhardt, G., Mauck, B., Hanke, W. & Bleckmann, H. (2001) Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). *Science* **293**, 102–104.
- Dral, A. D. G. (1977) On the retinal anatomy of cetacea (mainly *Tursiops truncatus*). In: *Functional Anatomy of Marine Mammals III*, R. J. Harrison (ed.), pp. 81–134. Academic Press, London.
- Erlinge, S. (1968) Food studies on captive otters *Lutra lutra* L. *Oikos* **19**, 259–270.
- Fasick, J. I., Cronin, T. W., Hunt, D. M. & Robinson, P. R. (1998) The visual pigments of the bottlenose dolphin (*Tursiops truncatus*). *Visual Neuroscience* **15**, 1–9.
- Fasick, J. I. & Robinson, P. R. (1998) Mechanisms of spectral tuning in the dolphin visual pigments. *Biochemistry* **37**, 433–438.
- Fasick, J. I. & Robinson, P. R. (2000) Spectral-tuning mechanisms of marine mammal rhodopsins and correlations with foraging depth. *Visual Neuroscience* **17**, 781–788.
- Flynn, J. J. & Nedbal, M. A. (1998) Phylogeny of the Carnivora (Mammalia): Congruence vs incompatibility among multiple data sets. *Molecular Phylogenetics and Evolution* **9**, 414–426.
- Gatesy, J. & O'Leary, M. A. (2001) Deciphering whale origins with molecules and fossils. *Trends in Ecology & Evolution* **16**, 562–570.
- Gerstein, E. R. (1994) The manatee mind: Discrimination training for sensory perception testing of West Indian manatees (*Trichechus manatus*). *Marine Mammals: Public Display and Research* **1**, 10–21.
- Gingerich, P. H., Wells, N. A., Russell, D. E. & Shah, S. M. I. (1983) Origin of whales in epicontinental remnant seas: New evidence from the early Eocene of Pakistan. *Science* **220**, 403–406.
- Green, J. (1977) Sensory perception in hunting otters. *Otters: Journal of the Otter Trust*, 13–16.
- Griebel, U. & Schmid, A. (1992) Color vision in the California sea lion (*Zalophus californianus*). *Vision Research* **32**, 477–482.
- Griebel, U. & Schmid, A. (1996) Color vision in the manatee (*Trichechus manatus*). *Vision Research* **36**, 2747–2757.
- Griebel, U. & Schmid, A. (2002) Spectral sensitivity and color vision in the bottlenose dolphin (*Tursiops truncatus*). *Marine and Freshwater Behaviour and Physiology*, **35**, 129–137.
- Hartman, D. S. (1979) Ecology and behavior of the manatee (*Trichechus manatus*). *American Society of Mammalogists Special Publication no. 5*, 153 pp.
- Herman, L. M. (1990) Cognitive performance of dolphins in visually-guided tasks. In *Sensory Abilities of Cetaceans*, J. Thomas & R. Kastelein (eds.), Plenum Press, New York.
- Jacobs, G. H. (1993) The distribution and nature of color vision among the mammals. *Biological Reviews* **68**, 413–471.
- Jacobs, G. H., Deegan, J. F., Neitz, J., Crognale, M. A., & Neitz, M. (1993) Photopigments and color vision in the nocturnal monkey, *Aotus*. *Vision Research* **33**, 1773–1783.
- Jagger, W. S. & Muntz, W. R. A. (1993) Aquatic vision and the modulation transfer properties of unlighted and diffusely lighted natural waters. *Vision Research* **33**, 1755–1763.
- Jamieson, G. S. & Fisher, H. D. (1971) The retina of the harbour seal, *Phoca vitulina*. *Canadian Journal of Zoology* **49**, 19–23.
- Jerlov, N. G. (1976) *Marine Optics*, 2nd Edn. Elsevier Co, Amsterdam.
- Kasprzyk, M. (1990) Zur spektralen Empfindlichkeit des Fischotters *Lutra lutra* (L., 1758). Dissertation, Naturwissenschaftliche Fakultät der Technischen Universität Carola-Wilhelmina zu Braunschweig.
- Kastelein, R. A., Zweypfenning, R. C. V. J. & Spekrijse, H. (1990) Anatomical and histological characteristics of the eyes of a month-old and an adult harbor porpoise (*Phocoena phocoena*). In: *Sensory Abilities of Cetaceans*, J. A. Thomas & R. A. Kastelein (eds.), pp. 463–480. Plenum Press, New York.
- Kirk, J. T. O. (1994) *Light and Photosynthesis in Aquatic Ecosystems*, 2nd Edn. Cambridge University Press, Cambridge.
- Kröger, R. H. H. (2000) Optical and developmental constraints on colour vision with lens eyes. *Journal of Optics A: Pure and Applied Optics* **2**, R39–R43.
- Kröger, R. H. H., Campbell, M. C. W., Fernald, R. D. & Wagner, H.-J. (1999) Multifocal lenses compensate for chromatic defocus in vertebrate eyes. *Journal of Comparative Physiology A* **184**, 361–369.
- Landau, D. & Dawson, W. W. (1970) The histology of retinas from the Pinnipedia. *Vision Research* **10**, 691–702.
- Lavergne, A., Douzery, E., Stichler, T., Catzeflis, F. M. & Springer, M. (1996) Interordinal mammalian relationships: evidence for paenungulate monophyly is provided by complete mitochondrial 12S rRNA sequences. *Molecular Phylogenetics and Evolution* **6**, 245–258.
- Lavigne, D. M. & Ronald, K. (1972) The harp seal, *Pagophilus groenlandicus* (Erleben, 1777). XXIII. Spectral sensitivity. *Canadian Journal of Zoology* **50**, 1197–1206.
- Lavigne, D. M. & Ronald, K. (1975) Pinniped visual pigments. *Comp. Biochem. Physiol.* **52B**, 325–329.
- Lavigne, D. M., Bernholz, C. D. & Ronald, K. (1977) Functional aspects of pinniped vision. In: *Functional Anatomy of Marine Mammals*, R. J. Harrison (ed.), pp. 135–173. Academic Press, New York.
- Levenson, D. H. & Schusterman, R. J. (1998) Pupillometry in seals and sea lions: Ecological implications. *Can. J. Zool.* **75**, 2050–2057.
- Levenson, D. H. & Schusterman, R. J. (1999) Dark adaptation and visual sensitivity in shallow and deep-diving pinnipeds. *Marine Mammal Science* **15**, 1303–1313.
- Levenson, D. H., Dizon, A. & Ponganis, P. J. (2000) Identification of loss-of-function mutations within the short-wavelength sensitive cone opsin genes of baleen and odontocete cetaceans. *Invest. Ophthalmol. Vis. Sci.* **41**(4), S 610.
- Loew, E. R. & McFarland, W. N. (1990) The underwater visual environment. In: *The Visual System of Fish* R. H. Douglas & M. B. A. Djamgoz (eds.), pp. 1–43. Chapman & Hall, London.
- Luck, C. P. (1965) The comparative morphology of the eyes of certain African Suiformes. *Vision Research* **5**, 283–297.
- Lythgoe, J. N. & Dartnall, H. J. A. (1970) A 'deep sea rhodopsin' in a mammal. *Nature* **227**, 955–956.

- Lythgoe, J. N. & Partridge, J. C. (1991) Visual pigments of teleost dichromats in green coastal water. *Vision Research* **31**, 361–371.
- Madsen, C. J. (1976) Tests for color discrimination and spectral sensitivity in the bottlenosed dolphin, *Tursiops truncatus*. *Ph.D. Thesis*, University of Hawaii.
- Madsen, C. J. & Herman, L. M. (1980) Social and ecological correlates of cetacean vision and visual appearance. In: *Cetacean Behavior*, L. M. Herman (ed.), pp. 53–100. Wiley, New York.
- Mass, A. M. (1992) Retinal topography in the walrus (*Odobenus rosmarus divergens*) and fur seal (*Callorhinus ursinus*). In: *Marine Mammal Sensory Systems* J. A. Thomas, R. A. Kastelein & A. Y. Supin (eds.), pp. 119–135. Plenum Press, New York.
- Mass, A. M. & Supin, A. Ya. (2000) Ganglion cell density and retinal resolution in the sea otter, *Enhydra lutris*. *Brain Behav. Evol.* **55**, 111–119.
- McFarland, W. N. (1971) Cetacean visual pigments. *Vision Research* **11**, 1065–1076.
- Muntz, W. R. A. (1972) Inert absorbing and reflecting pigments. In: *Handbook of Sensory Physiology, Vol. VIII: Photochemistry of Vision*, H. J. A. Dartnall (ed.), pp. 529–565. Springer Verlag, Berlin.
- Nagy, A. R. & Ronald, K. (1975) A light and electron-microscopic study of the structure of the retina of the harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). *Rapp. P.-v. Reun. Cons. Int. Explor. Mer.* **169**, 92–96.
- Partridge, J. C. (1990) The colour sensitivity and vision of fishes. In: *Light and Life in the Sea*, P. J. Herring, A. K. Campbell, M. Whitfield & L. Maddock (eds.), pp. 167–184. Cambridge University Press, Cambridge UK.
- Peichl, L. & Moutairou, K. (1998) Absence of short-wavelength sensitive cones in the retinae of seals (Carnivora) and African giant rats (Rodentia). *European Journal of Neuroscience* **10**, 2586–2594.
- Peichl, L., Behrmann, G. & Kröger, R. H. H. (2001) For whales and seals the ocean is not blue: a visual pigment loss in marine mammals. *European Journal of Neuroscience* **13**, 1520–1528.
- Peichl, L., Kovacs, K. M. & Lydersen, C. (2002) Absence of S-cones in the retinae of further marine mammals (whales and seals). *2002 Annual Meeting of the Association for Research in Vision and Ophthalmology (ARVO)*, abstract no. 3762 [2002 Annual Meeting Abstract and Program Planner accessed at www.arvo.org].
- Perez, J. M., Dawson, W. W. & Landau, D. (1972) Retinal anatomy of the bottlenosed dolphin (*Tursiops truncatus*). *Cetology* **11**, 1–11.
- Piggins, D., Muntz, W. R. A. & Best, R. C. (1983) Physical and morphological aspects of the eye of the manatee *Trichechus inunguis* NATTERER 1883: (Sirenia: mammalia). *Marine Behaviour and Physiology* **9**, 111–130.
- Pilleri, G. (1964) Zur Morphologie des Auges vom Weißwal. *Delphinapterus leucas* Pall (1776). *Hvalradets skrifter* **47**, 3–16.
- Pilleri, G. (1967) Retinafalten im Auge von Wassersäugetieren. *Experientia* **23**, 54–55.
- Pilleri, G. & Wandeler, A. (1970) Ontogeny and functional morphology of the eye of the fin whale *Balaenopterus physalus*. *Investigations on Cetacea* **2**, 179–229.
- Pütter, A. (1903) Die Augen der Wassersäugethiere. *Zoologische Jahrbücher, Abteilung Anatomie und Ontogenie* **17**, 99–402.
- Reitner A., Sharpe, L. T. & Zrenner, E. (1991) Is colour vision possible with only rods and blue-sensitive cones? *Nature* **352**, 798–800.
- Robinson, P. R. & Newman, L. A. (2002) An investigation of the color vision of marine mammals. *2002 Annual Meeting of the Association for Research in Vision and Ophthalmology (ARVO)*, abstract no. 4544 [2002 Annual Meeting Abstract and Program Planner accessed at www.arvo.org].
- Rochon-Duvigneaud, A. (1940) L'oeil des Cétacés. *Archives du Museum National d'Histoire Naturelle, Ser.* **6**, 16, 57–90.
- Ronald, K. & Lee, J. (1981) The spectral sensitivity of a polar bear. *Comp. Biochem. Physiol.* **70A**, 595–598.
- Southall, K. D., Oliver, G. W., Lewis, J. W., Le Boeuf, B. J., Levenson, D. H. & Southall, B. L. (2002) Visual pigment sensitivity in three deep diving marine mammals. *Marine Mammal Science* **18**, 275–281.
- Supin, A. Ya., Popov, V. V. & Mass, A. M. (2001) *The Sensory Physiology of Aquatic Mammals*. Kluwer Academic Publishers, Boston/Dordrecht/London.
- Szél, Á., Röhlich, P., Caffé, A. R. & van Veen, T. (1996) Distribution of cone photoreceptors in the mammalian retina. *Microsc. Res. Techn.* **35**, 445–462.
- Wartzok, D. & McCormick, M. G. (1978) Color discrimination in a Bering Sea spotted seal, *Phoca largha*. *Vision Research* **18**, 781–784.