

VISUAL OPTICS. IT'S WHAT THE EYE WAS DESIGNED FOR!

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1. LIGHT

The nature of light has long been a subject of controversy. Light has alternately been described as a wave (first proposed by Huygens in 1678) or as photon particles (first proposed by Newton in 1672). These descriptions are not mutually exclusive. Quantum optics, first proposed by Planck, uses both models to explain the dual nature of light and its interaction with matter. Both models also are applicable in the eye: the wave theory explains the physical changes light undergoes during its passage through the eye, and the particle theory explains the energy transformation that occurs when light strikes the photoreceptors.

Light behaves as a wave as it passes through transparent media such as air, vacuum, or the visual axis of the eye. Much like a wave of water, a wave of light has two principal characteristics. Its amplitude, A , is the maximum value of the field generated by the propagating wave; it determines the wave's intensity. The wavelength, λ , is the distance between adjacent wave crests; it determines the wave's location in the electromagnetic spectrum. As slide #3 shows, light, which is the visible portion of the electromagnetic spectrum, occupies a small fraction of that spectrum, which ranges from cosmic and gamma rays ($\lambda < 10^{-10}$ meters) to power transmission ($\lambda > 10^5$ meters). In humans, visible light normally ranges in wavelength from 390 (i.e., deep blue) to 760 (i.e., deep red) nm. However, additional wavelengths, outside the 390-760 nm spectrum, can be seen by other species. For example, many avian species possess ultraviolet vision that allows them to detect light with $\lambda < 300$ nm, thus enabling them to see hues that we cannot perceive. This capability is used both in foraging and selection of mates. At the other end of the spectrum, fish living in black-water rivers, in which the maximally transmitted light is longer than 600 nm, have evolved infrared vision, enabling them to detect light with $\lambda > 760$ nm that is prevalent in their environment. This is not to be confused with the infrared "vision" of snakes, however, which relies on the heat-detection properties of the pit organs.

On the other hand, light also possesses the properties of particles, which manifest as it is generated (at the light source) and absorbed (e.g., by the retinal photoreceptors). These nonmaterial particles, which are termed *photons*, represent quanta of energy that can be emitted or absorbed. The amount of energy in a given photon is inversely proportional to its wavelength; therefore, blue light, which has a shorter wavelength than red light, possesses more energy than the latter. The light energy of the photon is absorbed by the visual chromophore molecule in the outer segment of the photoreceptor (provided that the chromophore is sensitive to that photon's wavelength). This energy is then used to isomerize the chromophore (from 11-*cis*-retinal into all-*trans*-retinal in the case of rhodopsin), thereby initiating conversion of a light stimulus into an electric signal. This process is called the *phototransduction process*, and is discussed in detail later in this chapter. The particle nature of light also manifests in other clinically important processes. Fluorescein molecules, for example, absorb photons of blue light and re-emit (i.e., fluoresce) photons with a lower energy content (in the yellow-green portion of the spectrum).

2. GEOMETRIC OPTICS

2.1 Refraction

In vacuum, light travels at a constant speed (c) of approximately 3×10^8 m/sec. As it strikes denser media, light undergoes three changes:

1. Its velocity is reduced,
2. Its wavelength shortens, and
3. It is bent (unless it struck the surface of the medium at a 90° angle).

These changes are expressed in the equation:

$$n = c/v = \lambda/\lambda_m$$

where n is the index of refraction (or bending); c and λ are the speed and wavelength, respectively, in vacuum; and v and λ_m are the velocity and wavelength, respectively, in the new medium. The amount of refraction that occurs as light passes from one medium to another is described by Snell's law and is determined by the angle of incidence and by the refractive indices of both media. Because various structures of the eye differ in their refraction indices, light is successively refracted (bent) as it passes from air through the precorneal tearfilm, cornea, aqueous humor, lens, and vitreous on its way to the retina.

2.2 Vergence

An object that bends (or refracts) light is called a lens. When a single ray of light strikes a lens, the ray undergoes simple refraction. Most objects or images, however, generate a pencil of light rays, rather than a single ray. When a pencil of rays strikes a lens, they spread apart (i.e., diverge) or come together (i.e., converge). Divergence, or negative vergence, occurs when light strikes a concave lens; convergence, or positive vergence, occurs when light strikes a convex lens. The vergence power (i.e., amount of bending) of a lens is measured in units called *diopters*. One diopter (D) is the verging power of a lens with a focal length (f) of one meter. In broader terms:

$$D=1/f.$$

The focal length of a lens is the distance between the center of the lens and the point at which parallel rays of light are brought into focus by that lens. The focal length of a lens is directly proportional to its curvature radius. Therefore, the verging power (or the diopter power) of the lens increases as its curvature increases. As slide 8 shows, a convex lens with a focal length of 0.1 m will have a power of +10 D ($D = 1/f = 1/0.1 \text{ m} = 10D$). A flatter, convex lens with a focal length of 0.2 m will be "weaker," with a power of +5 D ($D = 1/f = 1/0.2 \text{ m} = 5D$). A concave lens with a focal length of 0.2 m will have a power of -5 D. The vergence powers of lenses in an optical system are additive. Thus, if the lens in slide 8 were placed next to each other, the resulting optical system would have a theoretical power of +15 D. If all three lenses in slides 8 & 9 were united into one system, it would have a power of +10 D. This principle holds in the eye, because the refractive contributions of the successive ocular surfaces are added to form a focused image on the outer segments of the photoreceptors.

The positive power of the convex lens indicates that it forms a *real image*, which means that incoming rays from the object are converged and focused on the other side of the lens (slide 8). The negative power of the concave lens indicates that it forms a *virtual or aerial image*, which means that the diverging rays are traced, using imaginary extensions, backward to a "focused" virtual image "located" on the same side of the lens as the object. These principles are manifested in ophthalmoscopy. The direct ophthalmoscope provides a real image of the patient's fundus, whereas indirect ophthalmoscopy entails use of a handheld convex lens and, therefore, provides a virtual image of the fundus.

2.3 Emmetropia and Ametropia

An *emmetropic* eye is one in which parallel light rays (from a distant object) are focused on the outer segments when the eye is at rest. A nonemmetropic, or *ametropic*, eye is one in which the focused image (from a distant object) falls anterior to the retina (i.e., near-sighted or myopic eye) or posterior to it (i.e., far-sighted or hypermetropic eye).

Few species are truly emmetropic, though once the values are corrected for eye size, many are within 1 D of emmetropia. In general, most mammals are within ± 1 D of emmetropia. Most selachians, amphibians, and snakes tend to be somewhat hypermetropic, while most cyclostomes and teleosts are myopic. There is a large variability, however, in the refractive values reported for some species. For example, reported values for the rat range from -13 D (i.e., myopic) to 20 D (i.e., hypermetropic), and in the horse, the reported range is -3 to 3 D. Such variation can be explained by the method used to refract the eye, skill of the examiner, accommodative state of both the animal and the examiner, sample size, and failure to correct for the artefact of retinoscopy. Results may also be influenced by breed, habitat, or working environment. It should be noted, however, that ametropia is not necessarily an evolutionary disadvantage. For example, animals dealing with close objects may find it advantageous to possess myopic refraction if this is combined with an accommodative mechanism permitting reflex emmetropia.

2.4 Aphakic Eyes and Intraocular Lenses

Because of the significant refractive role of the lens, cataract surgery (or any surgical lens extraction) resulting in aphakia leaves the eye severely hypermetropic. The aphakic eye lacks the refractive contribution of the lens; therefore, light is not sufficiently refracted, resulting in an image formation “behind” the retina. Since the early 1980s, veterinary ophthalmologists have sought to alleviate this problem by implanting intraocular lenses (IOLs) in the eyes of dogs following cataract extraction. The purpose is to compensate for loss of refraction by the lens, thereby returning the eye to an emmetropic state. Early attempts using 14.5 to 29.0 D IOLs left the eyes hypermetropic. Today, following the results of studies involving large numbers of dogs of various breeds, the consensus is the ideal IOL for dogs should have a power of 40.0 to 41.5 D. The 1.5-D range of recommended values probably results from breed differences. However, it is important to note that though 41D IOL's are used to bring aphakic dogs to emmetropia, this does *not* mean that aphakic dogs suffer from hypermetropia of 41D. Indeed, the hypermetropia in aphakic dogs has been shown to range from 14.4 to 15.2D. The reason that a 41D IOL is needed to correct 15D of hypermetropia is that an IOL is placed in the capsular bag, surrounded by aqueous humor. This environment results in a reduction of its overall refractive power (due to the small difference in refractive indices between the aqueous humor and the IOL), and therefore this power has to be higher than the aphakia it is intended to resolve. If dogs were to be fitted with spectacles to correct aphakia, then indeed these spectacles would require 15D lenses!

2.5 Spherical aberrations

The eye is not a perfect optical system. Indeed, Duke-Elder quotes Hermann von Helmholtz, the 19th century German physicist who invented the ophthalmoscope, as saying that “if an optician should try to sell me an instrument possessing such faults, I would feel justified in using the most severe language with regard to the carelessness of his work and return the instrument under protest”. Two of the most significant optical problems that affect the eye are spherical and chromatic aberrations. Positive *spherical aberrations* result from the fact that in both the cornea and the lens, rays passing through the periphery are refracted more than rays passing through the center. Therefore, rays passing through the periphery are focused closer to the cornea (or lens) than rays passing through its center. In other words, the focusing of rays depicted in slide 8 is an “ideal” refraction that does not take place in the eye. In the eye, there is a difference between the focal points of the peripheral and central rays, a difference that is called a “spherical aberration”, and which is measured in Diopters.

Both the cornea and the lens possess anatomical adaptations that are intended to minimize the extent of their inherent spherical aberrations. In the lens, the higher refractive index of the lenticular nucleus increases the refractive power of the central lens. This results in moving its focal point closer to the lens, closer to the focal point of the peripheral lens. A gradient variation in the refractive index of the lens would result in the formation of a multifocal lens, with further attenuation of the spherical aberration. Corneal spherical aberrations are minimized because the peripheral cornea is flatter than the central (apical) cornea. This decreases the refractive power of the peripheral cornea, and moves its focal point (away from the cornea and) closer to that of the central cornea. Therefore, refractive surgeons attach great importance to centering the apical cornea, so that the aberration-free zone is aligned with the pupil, thereby contributing to a high quality retinal image. The possible effects of corneo-scleral transpositions on visual optics in our animal patients have yet to be investigated.

Another structure that plays a critical role in reducing spherical aberrations is the pupil. Contraction of the pupil blocks rays of light that entered the eye through the most peripheral (and refractive) cornea. It also prevents light from passing through the peripheral lens. Thus, miosis allows only rays that pass through the central cornea and lens to reach the retina, and thereby it contributes to the formation of a well-focused image. A mydriatic pupil, on the other hand, allows more peripheral rays to enter the eye, and their passage through the peripheral cornea and lens increases the amount of spherical aberrations. In humans, an 8 mm pupil induces 1D of spherical aberrations, which is the reason for the significant blurring of vision that we experience after our pupils have been pharmacologically dilated.

3. VISUAL OPTICS

3.1 Refractive Structures of the Eye

As mentioned, light is successively refracted by the various ocular structures as it passes through the eye on its way to the retina. The most anterior optical surface of the eye is the precorneal tear film. By strict definition, it could be argued that the tear film is the most refractive layer of the eye. This is because of the large difference in refractive indices as light passes from air, which has a refractive index of almost 1, into the tear film, which has a refractive index of 1.336. Factoring the refractive indices of air and the tear film into Snell's law reveals that the precorneal tear film has a refractive power of 43D. Alterations in the composition or breakup time of the tear film may change the refractive power of the eye by as much as 1.3 D, and may contribute to the blurry vision complaints commonly encountered in (human) dry eye patients. The effect of tear deficiencies on the quality of vision in our animal patients has yet to be studied.

The cornea is the next organ through which incoming light passes. The corneal stroma has a refractive index of 1.376. Because this value is slightly higher than the refractive index of the tear film, passage of light from the tear film into the anterior layers of the cornea results in an additional 5 D of refractive power. However, these 5 D are "lost" when light passes from the posterior cornea into the aqueous humor, which has a refractive index nearly identical to that of the tears. When combined, the precorneal tear film and the cornea contribute a net refractive power of 43 D, which conventionally (though somewhat erroneously) is attributed to the cornea. Therefore in humans, for example, the cornea contributes approximately 70% of the total 60 D power of the eye, thus making it our largest refractive organ.

Another factor affecting the refractive power of the cornea, besides the refractive index, is its curvature. Because the cornea converges light, it acts as a convex lens. As stated earlier, the refractive power of such a lens depends to a large extent on its curvature radius. Therefore, in large eyes, which are characterized by flat corneas, the refractive

power of the cornea is reduced. Conversely, in small eyes with spherical corneas, its power is increased. Slide 23 shows the relationship between size of the eye and refractive power of the cornea in several species. Furthermore, the central and peripheral corneas have different curvatures, and consequently differ in their refractive powers (see “spherical aberrations” above).

As noted, the refraction that occurs as light passes from the cornea into the aqueous humor, and during its passage through the aqueous, has little overall significance. Therefore, the next significant refractive structure through which light passes after the cornea is the pupil. The pupillary aperture is not considered to be a classic refractive structure, but it does make an important contribution to the resolving power of the eye. As the pupil dilates in dim light, the number of photons entering the eye increases, thereby also increasing retinal illumination. Mydriasis, however, also decreases the depth of focus of the eye. This is especially critical in animals with limited accommodative capability (discussed later). The implication for such species is that as the pupil dilates, the range of distances at which objects remain in focus decreases. For example, with an eye that is focused at a distance of 1 m, objects at a distance of between 0.56 and 5.00 m will be in focus when pupil diameter is 1 mm; the range decreases to between 0.78 and 1.40 m when the pupil dilates to 4 mm. Furthermore, as the pupil dilates, the relative significance of optical aberrations inherent in the eye increases (discussed later), thereby reducing its resolving power. Therefore, the pupillary light reflex is, in effect, a constant balancing of two conflicting requirements for vision: maximal retinal illumination, and visual resolution. As a rule of thumb, constricting the pupil by half increases visual resolution by a factor of two.

The lens is another structure that makes a significant contribution to the overall refractive power of the eye. As in the case of the cornea, the refractive power of the lens is determined both by its refractive index and by its curvature. In humans and in many nonaquatic species, the refractive index of the lens is ~1.41. Since this refractive index is relatively similar to that of the aqueous humor (range, in most species, 1.334–1.338), the lens in these species has a rather low refractive power. In humans, the calculated refractive power of the lens is approximately 19 D. The refractive index of the lens increases in aquatic species, where it can be as high as 1.65, resulting in significantly higher refractive power.

The second factor determining lenticular refractivity, the lens curvature, also differs between aquatic and non-aquatic species. Generally, it can be said that the lens is spherical in fish and aquatic mammals, while it is more discoid in terrestrial species. Therefore, it will have a higher refractive power in the former, compared to the latter. The reasons for the effect of habitat on the refractive index and curvature of the lens are discussed in the section on aquatic species below. Of course, the curvature (and, hence, the refractive power) of the lens can also be changed actively through a process termed *accommodation* (see below).

Though usually forgotten by practitioners, the vitreous also plays an important role in refractive development of the eye. Vitreous elongation increases the axial length of the eye, thereby increasing the refractive path of light and inducing myopia. In certain species of fish, this mechanism serves to increase ocular refraction and compensate for loss of corneal refractive power. In different goldfish strains, for example, the vitreous body can contribute anywhere from 37% to 70% of the total axial length of the eye. In visual-deprivation studies conducted during critical developmental periods in species as varied as chickens, fish, and tree shrews, the deprivation-induced myopia also was a result of elongation of the vitreous.

3.2 Accommodation

Accommodation is a rapid change in the refractive power of the eye, which is intended to bring the images of objects at different distances into focus on the retina. The stimulus for the accommodative response is a blurred, or defocused, retinal image. Eyes of vertebrates accommodate by one or more of the following mechanisms: changing the corneal curvature, changing the distance between the cornea and retina, changing the curvature or position of the lens, or by having two or more separate optical pathways of different refracting power.

Humans and other primates accommodate by changing the curvature of the lens. To view distant objects, sympathetic innervation induces relaxation of the ciliary body muscle, which in turn leads to stretching of the lens zonules. The increased tension of the zonules results in a greater pull on the lens capsule, thus causing the lens to become more discoid and decreasing its overall axial thickness and refractive power in a process of *disaccommodation*. To accommodate for near objects, the reverse process takes place. Parasympathetic input induces contraction of the ciliary body muscles, leading to relaxation of the zonular fibers and reduced tension on the lens capsule. In turn, this liberates the inherent elasticity of the lens, thus resulting in a more spheroid lens possessing greater axial thickness and refractive power. These changes in lenticular curvature allow primates such as the young (<5 years) rhesus monkey to accommodate by as much as 34 D. As the animal ages, however, it gradually loses its accommodative capability in a process termed *presbyopia*, and monkeys older than 25 years can accommodate only to an average of 5 D. A similar and dramatic reduction has been reported in the chicken, as lenticular accommodation decreases from > 20D at hatching to <5D at one year of age. Mechanisms proposed for presbyopia include reduction in ciliary muscle contractility, changes in the refractive index of the lens, age-related changes in the relative position of the lens and ciliary body, and loss of the lens capsule and lens fiber elasticity.

As with most other aspects of vision research, the mammalian species in which accommodative capabilities have been studied most extensively is the cat. The elasticity of the feline lens capsule is 5% of the elasticity in humans; thus, the cat obviously does not accommodate by changing its lens curvature. Instead, *translation* (i.e., the anteroposterior movement of the entire lens) is responsible for accommodative changes in the feline eye. This movement is made possible by the relative abundance of meridional (i.e., longitudinal) fibers in the feline ciliary body muscle and by the relative scarcity of circular fibers, which predominate in primates. Parasympathetic stimulation of the meridional muscle fibers in the cat results in forward displacement of the lens by up to 0.6 mm, thus inducing anywhere between 2 and 8 D of accommodation. The dog's accommodative power is reportedly lower, only 1 to 3 D in range. However, in other carnivores, the same mechanism is used to achieve a significantly greater magnitude of accommodation (usually associated with primates). Forward lens movement in the raccoon induces accommodation of up to 19 D, which is the greatest accommodative capability of any nonprimate, terrestrial mammal studied. A similar wide range of accommodative capability also exists in other closely related species. For example, the grey squirrel does not accommodate, whereas the California ground squirrel can accommodate up to 6 D. It should be noted that lens displacement in mammals results from ciliary muscle contraction, but in fish, such displacement is affected by a specialized smooth muscle, the retractor lentis.

Another species in which accommodation has been studied extensively is the chicken, which employs several accommodative mechanisms. Lenticular accommodation in the chicken is achieved when the ciliary or peripheral iris muscles contract. This contraction is transmitted through the ciliary processes, and results in changes similar to those that occur in primates. These changes include thickening of the lens by 0.2 mm, steepening of its curvature, and a bulging of the lens into both the anterior and vitreous chambers (thereby reducing their depths). However, unlike mammals, chickens also possess a mechanism for changing the corneal curvature. Just like lenticular accommodation, corneal accommodation in the chicken also results from ciliary muscle contraction, which flattens of the peripheral cornea and increases the curvature of the central cornea. Corneal accommodation is reported to play an important role in chicken accommodation, contributing 8–9 D compared to 15-19D of lenticular accommodation, though other researchers claim the contribution is insignificant. Changes in intraocular pressure do not contribute to lenticular accommodation in the chicken, but they may contribute to changes in refractive power brought about by choroidal stretching. It should be noted that the chicken, as well as other avian and reptile species, may accommodate independently in both eyes, thus resulting in *anisometropia* (i.e., unequal degree of refraction in the two eyes) of up to 6 D.

3.3 Emmetropia Underwater

In aquatic species, the cornea is in contact with water rather than air. Because of the very small (~0.003) difference between the refractive indices of the cornea and water, the cornea of these species has virtually no refractive power. Fish are forced to compensate for this absence by increasing the refractive power of other ocular structures, usually the lens. For this reason, as noted earlier, the lenses of fish eyes are very spherical. Their increased curvature results in significantly larger refractive power. Biochemical changes in lenticular proteins also increase the refractive index of the fish lens, thereby contributing to significant refraction as light passes from the aqueous humor into the lens. These evolutionary adaptations can increase the refractive power of the lens to as much as 500 D! If it were not for these two lenticular adaptations, the absence of corneal refraction would cause fish to be severely hypermetropic underwater.

The problem of refraction underwater is further complicated in species that move in and out of water. This is because it is physically impossible for an eye to be emmetropic both in air and underwater. Eyes that are emmetropic in the air will be hypermetropic underwater, as the refractive power of the cornea is lost due to its submersion in water. Conversely, eyes that are emmetropic underwater become extremely myopic in the air, as the cornea (due to Snell's law) contributes refraction that the eye did not possess underwater. Therefore, species that live and function in both habitats must "choose" whether they will be emmetropic in the air or underwater. It is very interesting to observe that both of these evolutionary strategies exist in the animal kingdom. Birds that hunt underwater, such as cormorants and penguins, are emmetropic in the air. These species overcome the resulting underwater hyperopia by increasing the accommodative power of the lens. During accommodation in the cormorant, for example, the lens bulges through the pupil, forming a lenticonus that increases the lenticular optical pathway and refractive power. This gives the lens in some diving birds an accommodative power of 60D, and an incredible accommodation rate of >600 D/sec, 10 times as fast as non-diving birds.

On the other hand, many aquatic mammals developed an opposing evolutionary strategy. Sea lions, harbor seals and other Pinnipeds are emmetropic underwater. Consequently, these animals become severely myopic when they come out of the water to breathe. Various mechanisms have evolved to make up for the increased refractive power of the eye in aerial environment. In some dolphin species, a specialized, flattened region with very low refractive power has evolved in the nasal cornea, providing for focused aerial vision, whereas the rest of the cornea is convex, providing for underwater vision. The animal shifts its head as it exits the water to allow light to enter through the flat "window". A similar solution, with different curvatures in different regions of the cornea, has evolved in both harbor seals and harbor porpoises. As the animal moves from water to air, the resulting miosis allows the iris to block light from highly refractive quadrants of the cornea from entering the eye; underwater, mydriasis allows light from these quadrants to enter the eye. In penguins, the entire cornea is flat, thus minimizing the alteration in refractive state when moving from air to water. In these animals, the cornea is the major refractory organ on land, and lens accommodation provides for underwater refraction. More primitive amphibians (e.g., crocodiles) that lack this compensatory accommodative capability simply cannot focus when submerged and rely on other senses when hunting underwater.

Rodents and ungulates are generally described as lacking accommodative capability. In the former, this lack of accommodation is explained by the absence of a well-defined ciliary muscle, though the small pupil size in species such as the rat does provide these animals with a great depth of focus. Lack of accommodation in ungulates, some of which possess a more developed ciliary muscle, is more difficult to explain and may account for the low visual acuity in such species as the cow. The horse has a much higher visual acuity than the cow, but its accommodative power is also limited to $\pm 1D$ in either direction.