Vision in dogs

Paul E. Miller, DVM, and Christopher J. Murphy DVM, PhD

Almost every dog owner, veterinary student, and veterinarian has wondered, on one occasion or another, how well dogs see. The question is more than a matter of intellectual curiosity, however, because a dog's visual capabilities directly affect its ability to engage in high performance, visually orientated activities, such as guiding the blind, police work, schutzhund, obedience training, racing, and hunting. Nevertheless, none of the currently available textbooks of veterinary ophthalmology provide a concise summary of the visual abilities of dogs, and the pertinent literature on canine vision is widely scattered throughout such diverse fields as psychology, physiology, optics, neuroanatomy, and electrophysiology. The purpose of this review was to collect and interpret the relevant literature on the visual abilities of normal dogs.

Fundamentals of Vision

Because a multitude of factors are involved in the sensation of vision, the outwardly simple question of how well dogs see is, in reality, quite complicated. The question can be partially answered by describing the visual acuity of dogs, their abilities to detect light or color, or the features of other individual visual parameters, but the complete visual experience is a synthesis of all of these constituent parts into a unified perception of the world. Because our current understanding of many components of canine vision is imperfect, so, therefore, will be any attempt to describe them. It is also important to recognize that, because of species differences in visual parameters, dogs probably perceive the world differently from the way that people do. Descriptions of the visual abilities of nonhuman species are, of necessity, couched in terms of human visual capabilities and, therefore, may not be perfectly accurate representations of how animals see.

The ability to perceive light and motion are generally regarded as the fundamental aspects of vision. However, other factors, such as visual perspective, visual field of view, depth perception, visual acuity, and the abilities to perceive color and form, also play important roles in how animals see.[1]

Sensitivity to Light

The canine visual system has adapted to exploit a particular ecological niche by enhancing visual performance under low light conditions but still retaining good function under a wide array of lighting conditions, including daylight. Therefore, the dog's visual system is not highly adapted for strictly diurnal or nocturnal conditions but, rather, has evolved for an arrhythmic photic existence.[1,2] The minimum threshold of light for vision in cats is approximately 6 times lower than that for normal human beings.[3] Although the minimum threshold of light for vision in dogs is assumed to be somewhat greater than that for cats, Pavlov concluded in the early part of this century that the ability of dogs to analyze the intensity of low-level illumination is so well developed that human experimenters are unable to determine its limits using their own senses.[1]

Dogs employ several methods of improving vision in dim light. Both dogs and humans use rod photoreceptors to function in dim light, but the central 25° of the retina in dogs consists predominantly of rods.[4] In people, this region consists predominately of cones, which are important for color vision and vision in bright light. The rod photopigment, rhodopsin, is also slightly different between dogs and humans. In dogs, rhodopsin has a peak sensitivity to light of wavelengths between 506 and 510 nm and, as is typical of species adapted to function well in dim light, takes over an hour to completely regenerate after extensive exposure to bright light.[4-6]

Rhodopsin in people, on the other hand, has a peak sensitivity to light of somewhat shorter wavelengths (approx 496 nm) and regenerates more quickly after exposure to bright light. The range of wavelengths to which rhodopsin in dogs is sensitive[4-6] suggests that the visible spectrum for dogs in dim light is similar to that of human beings, and that the enhanced night vision in dogs, relative to humans, is not due to differences in the range of wavelengths of light to which dogs and people are sensitive.

The superiorly located reflective tapetum lucidum also enhances the dog's ability to detect objects in dim light. Presumably, it does so by reflecting light that has already passed through the retina back through it a second time, thus providing the photoreceptors at least 2 chances at capturing each quantum of light. This reflection of light, however, has its price, as scattering of light during this process may reduce the ability of the eye to precisely resolve the details of an image.[7]

Anatomically, the tapetum lucidum in dogs is a highly cellular structure that is between 9 and 20 layers thick at its center and is rich in zinc and cysteine.[7-12] The variety of colors seen in the region of the tapetum lucidum during ophthalmoscopy result from the differential interaction of light with the tapetum's physical structure rather than from the inherent spectral composition, or color, of its pigments.[13] The tapetum is an efficient reflector of light; 1 study has suggested that the feline eye reflects about 130 times more light than does the human eye.[14] Because of anatomic differences, the

From the Comparative Ophthalmology Research Laboratories, Department of Surgical Sciences, School of Veterinary Medicine, University of Wisconsin, 2015 Linden Dr W, Madison, WI 53706-1102.

The authors thank Marie Nelson for assistance with figures, and Dr. Gustavo Aguirre (James A. Baker Institute for Animal Health, Cornell University), Dr. Donald Mutti (School of Optometry, University of California-Berkeley), Dr. Jay Neitz (Department of Cellular Biology and Anatomy, Medical College of Wisconsin), Dr. Jacob Sivak (School of Optometry, University of Waterloo), Dr. Peter Spear (Department of Psychology and Center for Neuroscience, University of Wisconsin-Madison), Dr. James Ver Hoeve (Department of Ophthalmology, School of Medicine, University of Wisconsin-Madison), and Dr. Karla Zadnik (School of Optometry, University of California-Berkeley) for review and suggestions.

canine tapetum is probably less efficient at reflecting light than is that of the cat, but its light-reflecting properties are still undoubtedly substantial.

The tapetum may not only reflect light. It has been suggested in cats and lemurs that tapetal riboflavin absorbs light in the shorter wavelengths (blue, approx 450 nm) and shifts it via fluorescence to a longer wavelength (520 nm) that more closely approximates the maximal sensitivity of rhodopsin in the rod photoreceptors.[15-17] This shift may brighten the appearance of a blue-black evening or night sky and, thereby, enhance the contrast between other objects in the environment and the background sky.[16] Additionally, it has been proposed that regional differences in reflection spectra (seen ophthalmoscopically as differences in regional coloration of the tapetum) may lead to local variations in the retinal spectral sensitivity. However, it is unclear whether this is important in living animals.[18] In a strain of Beagles in which a hereditary tapetal degeneration was identified, it was observed during electrophysiologic testing that affected dogs had a slightly reduced sensitivity to white light, compared with unaffected dogs.[9] In our experience, however, dogs that lack a tapetum do not appear clinically to have impaired vision in dim lighting circumstances. Similarly, dogs that lack pigmentation in the non-tapetal zone and, therefore, presumably have exaggerated scattering of light inside the eye do not appear to have clinically significant reduced visual acuity in bright light. However, the visual abilities of dogs with atapetal and subalbinotic fundi have not yet been precisely measured, and it is possible that differences in visual abilities associated with variations in the appearance of the tapetum may be discernable in the future with more rigorous testing.

Albinism, the complete absence of light-absorbing pigment, is well documented in many species and is associated with impaired visual function.[19] True albinism is rare in dogs, but an Australian Shepherd with ocular albinism did have photophobia, presumably from increased light scattering within the eye.[20] Abnormalities in the fovea (in species that possess one) and central visual pathways have also been reported in albinos.[19] The effect of albinism on the visual system in dogs has not been critically evaluated.

The canine visual system has also adapted to perform adequately in bright light and when there is a marked difference in luminance between different regions of the retina. Typically, the superior part of the retina receives light from the darker ground, and the inferior part receives light from the brighter sky. In some instances, however, the sky is darker and the ground is highly reflective (eg, when it is covered with snow or sand) and, therefore, brighter than the sky. Several mechanisms allow dogs (and people) to maintain visual function under these situations of greatly varying lighting intensities. Reflexive adjustment of pupil size; unconscious alteration of the overall, and perhaps regional, sensitivity of the rods; and recruitment of cone photoreceptors, which are adapted for use in bright light, improve the dog's visual performance in bright light. Additionally, it has been suggested that specialized retinal amacrine cells, which bridge the inferior and superior portions of the retina,[21] help to equilibrate differences in incident illumination among the areas of the retina. The extent of this equilibration, if it does occur, is unclear, and equilibration may be confined to only a narrow zone in the horizontal meridian. The superiorly located reflective tapetum lucidum may also enhance the view of the usually darker ground, and the inferiorly located, usually darkly pigmented, tapetum nigrum may reduce light scattering originating from the usually brighter sky.

Sensitivity to Motion

Although little work has been done on the motion-detecting abilities of dogs, it is probable that the perception of movement is a critical aspect of canine vision[1] and that dogs, like people, are much more sensitive to moving objects than they are to stationary ones. The dominant photoreceptor in dogs, the rods, are particularly well suited for detecting motion and shapes. In a 1936 study of the visual performance of 14 police dogs, the most sensitive dogs could recognize moving objects at a distance of 810 to 900 m, but could recognize the same object, when stationary, at a distance of only 585 m or less.[2]

Sensitivity to Flickering Lights

Although not related to motion detection, the point at which rapidly flickering light appears to fuse into a constantly illuminated light (flicker fusion) provides insight into the functional characteristics of the rods and cones in dogs. The flicker frequency at which fusion occurs varies with the intensity and wavelength of the stimulating light.[22-25] Results of electroretinographic studies of anesthetized dogs suggest that canine rods can detect flickering up to a maximum of approximately 20 Hz,[22,23] which is similar to the maximum for human rods.[24,25] With more intense light, cone photoreceptors are activated, and flicker fusion occurs at around 70 Hz in dogs as measured electroretinographically.[22,23] Behavioral testing of 4 Beagles trained to press a key when the test light was perceived to be flickering demonstrated that unanesthetized dogs could detect flicker at moderately higher frequencies (70 to > 80 Hz) and at lower levels of light intensity than the results of electroretinography would suggest.[26] The flicker fusion frequency for human cones (approx 50 to 60 Hz for luminous spots[27]) is reportedly lower than that for canine cones, but some people are capable of detecting flicker up to approximately 70 Hz.[24,25] Because of this heightened sensitivity to flicker, a television program, in which the screen is updated 60 times/s and appears as a fluidly moving story line to most humans, may appear to rapidly flicker to dogs.

Visual Perspective

Obviously, height of the eyes above the ground has a major impact on the perception any animal has of its environment, and visual perspective in dogs is oriented considerably closer to the ground than it is in people. On the other hand, shoulder height in dogs ranges from < 8 inches to > 34 inches.[28] A field of tall grass may appear to be a daunting array of impenetrable brush to a Shih Tzu, whereas an Irish Wolfhound may experience no difficulty in visually orienting itself in the same field (Fig 1). Some breeds, such as the English Springer Span-

Figure 1—The effect of visual perspective on vision. The same scene as viewed by a small dog with eyes located 8 inches above the ground (top), a tall dog with eyes 34 inches above the ground (middle), and a person with eyes 66 inches above the ground (bottom).

iel, appear to have developed behavioral traits, such as leaping into the air while visually searching for objects, that perhaps enhance their visual perspective. The lack of morphologic standardization among breeds and individuals is doubtless a contributing factor as to why the visual system of dogs has not been more intensively studied.

Visual Field of View

Though not critically evaluated, the extent of the visual field in dogs (ie, the area that can be seen by an eye when it is fixed on 1 point) also varies by breed, as there are marked variations among breeds in the placement of the eyes in the skull and, thereby, in the orbital

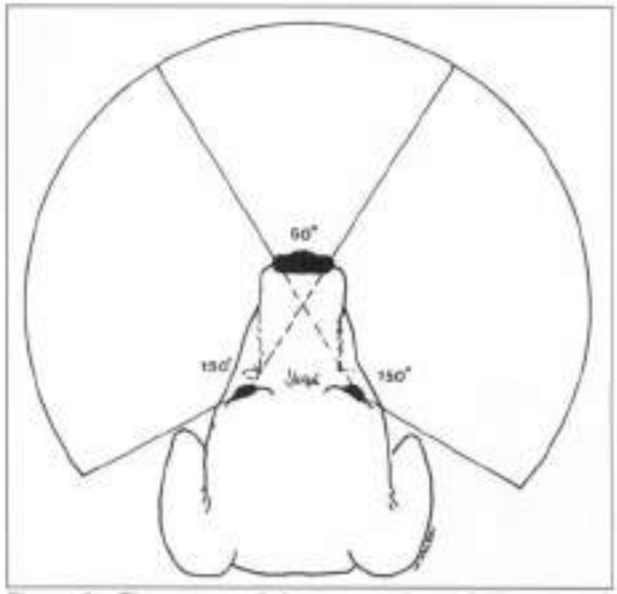

Figure 2—The extent of the monocular and binocular visual fields in a typical mesocephalic dog.

axis.[13] In the brachycephalic breeds, the eyes are more laterally directed, and the extent of the visual field and amount of binocular overlap are probably different from the visual field and binocular overlap in mesocephalic breeds, in which the eyes are directed more forward.[13] Length of the nose would also interfere with the amount of binocular overlap. In dogs, the eyes typically are placed so as to deviate approximately 20° lateral to the midline, whereas in people, the eyes do not deviate but look straight ahead.[1] When the 2 eyes are considered together, the visual field of the typical dog has been estimated, on the basis of calculations from morphologic data, to be approximately 250°.[2] In 1 study,[29] two 20 kg mixed-breed dogs with average length noses were trained to fixate on 1 visual stimulus and react to a second stimulus introduced in a limited area of their peripheral visual field. Visual fields for these dogs was estimated to be 240°.[29] These estimates suggest that, with each eye, the typical dog can see from 120° ipsilateral to between 15 and 30° contralateral, for a total monocular field of view of 135 to 150° (Fig 2).[29] Therefore, the field of view of the average dog is approximately 60 to 70° greater than that of people, and this provides dogs with a greater ability to scan the horizon. However, the degree of binocular overlap is greater in people than it is in dogs.

Depth Perception

Depth perception is enhanced in those regions in which the visual fields of the 2 eyes overlap. Reported estimates of the degree of binocular overlap in dogs vary widely, and binocular overlap may differ by breed. The extent of binocular overlap was estimated to be between 30 and 60° in behavioral studies,[29] was calculated to be between 35 and 40° on the basis of ganglion cell density,[30] and was reported to be approximately 80 to 116° on the basis of optical considerations.[1,2] It is probable that calculations based on optical considerations overestimate the extent of binocular overlap in dogs, because

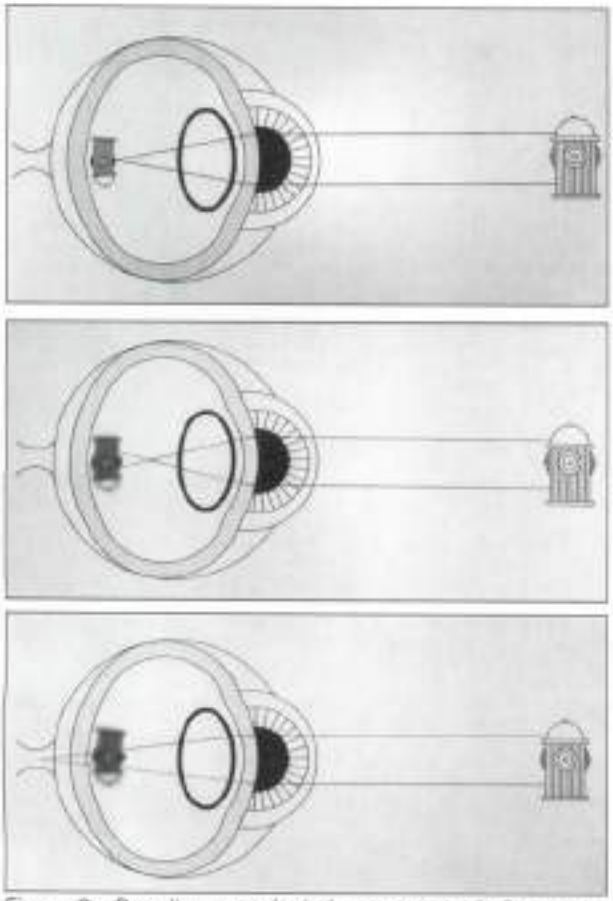

Figure 3—Ray diagrams depicting emmetropia (ie, proper focusing of images on the retina; top), myopia (near-sightedness, or focusing of images in front of the retina; middle), and hyperopia (far-sightedness, or focusing of images behind the retina; bottom). German Shepherds, Rottweilers, and Miniature Schnauzers are predisposed to myopia.[38]

the nose blocks more of the temporal retina's view of the nasal visual field than anticipated,[29] and that the extent of binocular overlap is most likely in the range of 30 to 60° for the average dog. For comparison, field of view in people is approximately 180°, and the degree of binocular overlap is approximately 140°.[2] In dogs, the monocular visual fields are wide, but the binocular field has been suggested to be tall, narrow, and pear-shaped.[2] Depth perception is probably greatest when dogs look straight ahead and is probably blocked by the nose in most breeds when dogs look below the horizontal.

However, merely viewing an object with both eyes simultaneously does not guarantee improved perception of depth. Stereopsis (binocular depth perception) results when the 2 eyes view the world from slightly different vantage points, and the resulting image is blended or fused into a single image. If the 2 images are not fused, double vision may result. It is the disparity between the 2 *resulting* retinal images that, when fused, provides clues that allow accurate discrimination of depth.[31] Nonconjugate movements of the eyes probably also provides clues for depth perception.[31]

Although binocular depth perception is superior if the images can be blended into 1, monocular depth perception is also possible.[31] Monocular clues relating to depth include relative brightness, contour, areas of light and shadows, object overlay, linear and aerial perspective, and density of optical texture.[31-33] In addition, movement of the head results in an apparent change in the relative positions of the objects viewed (a phenomenon known as parallax) and, thereby, produces the sensation that the elements in the visual environment are moving at different speeds, allowing depth to be estimated. Puppies were shown to have excellent monocular and binocular depth perception in a controlled experiment evaluating avoidance of a visual cliff.[35] Adult dogs probably have even better visual abilities than young puppies, because the canine retina and tapetum do not mature until several weeks to months of age.[34]

On the basis of studies of retinal ganglion cell topography, it has been hypothesized (although not experimentally verified) that depth perception may be impaired in the peripheral 15° of the right and left portions of the area of binocular overlap in dogs because of a lack of alpha (also referred to as "Y") ganglion cells in the corresponding areas of the retina.[30] Therefore, the area of the retina available for high-quality depth perception may be smaller than the area estimated on the basis of binocular overlap. Nevertheless, depth perception in dogs is clearly sufficient for their lifestyle. They easily judge distances visually, as evidenced by their ability to catch fast-moving objects and clear hurdles.

Visual Acuity

When dogs are said to see well in dim light, what is meant is that canine visual sensitivity in reduced levels of light is quite high,[2] and that dogs have relatively good visual acuity under those circumstances. Visual acuity, however, is different from sensitivity to dim light, and refers to the ability to see the details of an object separately and unblurred.[2] Visual acuity depends on the optical properties of the eye (ie, the ability of the eye to generate a precisely focused image), the retina's ability to detect and process images, and the ability of higher visual pathways to interpret images sent to them.[2] In general, visual acuity in dogs is believed to be limited by the retina and not by the optical properties of the eye or by postretinal neural processing in the brain.[35] Nevertheless, these 2 factors can become the limiting step in visual discrimination in many pathological conditions such as myopia, when corrective lenses are required to see clearly, or when higher CNS visual pathways are impaired. Postretinal neural processing has been extensively investigated in cats, but much less so in dogs, and is beyond the scope of this review.

Optical factors in visual acuity—The optical qualities of the canine eye have been investigated by several authors,[36-40,a] and a schematic eye that allows mathematical predictions of the optical capabilities of the canine eye has been constructed.[41] The optical media of the eye, namely the cornea, aqueous humor, lens, and vitreous humor, are responsible for creating a properly focused image on the retina. In a normally focused (emmetropic) eye, parallel rays of light (such as those from a distant object) are focused on the retina. If parallel rays of light are focused in front of the retina, myopia (nearsightedness) results. If they are focused behind the retina, hyperopia (farsightedness) results (Fig 3). Such errors in refraction are usually expressed in units of optical power called diopters. The extent of the error can be expressed by the formula diopters = 1/f, where f = the focal length (in meters) of either the lens or optical system as a whole. Therefore, if an eye is said to be 2 diopters myopic at rest, it is focused at a plane located ½ m in front of the eye. Similarly, an eye that is emmetropic at rest, but can accommodate (change focus) 3 diopters is capable of clearly imaging objects on the retina that range from as far away as the visual horizon (infinity) to as near as ⅓ m in front of the eye.

Sensory clues such as smell or sound, in addition to vision, may help dogs to better characterize nearby items in their environment. This penchant for using smell to identify objects that are very close can lead to the mistaken belief that dogs are normally nearsighted or myopic. This is clearly not the case. In a survey of 240 dogs, it was found that the average resting refractive state was within 0.25 diopter of emmetropia.[36] There were individuals in this large population, however, that were significantly myopic, and there was a distinct tendency towards development of myopia with greater age and development of nuclear sclerosis.[36] This mild shift in resting focus of the eye needs to be distinguished from age-related presbyopia, which is the loss of focusing (accommodative) ability that affects all middle-aged humans (and probably dogs). The prevalence, degree, and importance of presbyopia in dogs has not been determined.

Breed predispositions to myopia also were found. In 1 study, 53% of German Shepherds in a veterinary clinic population were myopic by −0.5 diopters or more, and 64% of all Rottweilers were myopic.[36] In contrast, only 15% of German Shepherds in a guide dog program were myopic, suggesting that dogs with visual disturbances such as nearsightedness do not perform as well as normally sighted dogs, and are often withdrawn from intense training programs by observant handlers.[36] For comparison, people with −0.75 to −2.0 diopters of myopia will typically complain of visual impairment and report improved vision with corrective lenses. Defocussing a human being by 2 diopters reduces visual acuity from 20/20 to 20/100,[42] and a comparable reduction in acuity has been reported for dogs.[43] Therefore, it may be reasonable to screen dogs performing visually demanding tasks, or those on which human life relies, for abnormalities in their refractive state (ie, whether they are nearsighted or farsighted, or have significant irregularities in their focusing abilities, such as astigmatism).[36,43]

In addition to myopia or hyperopia, other optical aberrations may result from imperfections in the refractive media and lead to degradation of the image formed on the retina. These aberrations may be quite simple or very complex in nature. Astigmatism occurs when different regions of the optical system fail to focus parallel rays of light in a uniform fashion. This can occur because of regional irregularities in the curvature of the cornea or lens that permit a light ray in 1 meridian to be focused differently from a light ray in another meridian. The result is warping of the image, an extreme example of which can be found in the irregular mirrors found at many fairs and carnivals. Astigmatism is generally uncommon in dogs, but has been observed in a variety of breeds since the early 1900s.[36,40,a] In a recent survey, astigmatism, which ranged from 0.5 to 3.0 diopters, was found in only 10 of 240 dogs, and was unilateral in 8 of the 10 dogs.[36]

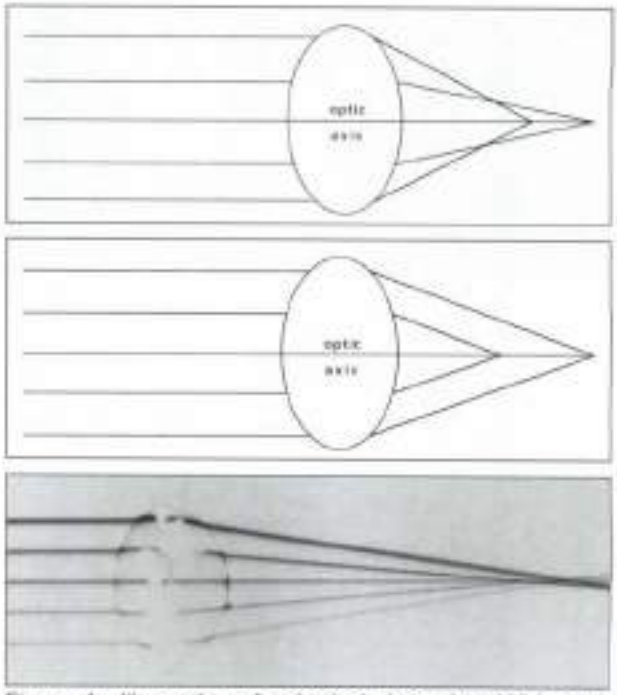

Figure 4—Illustration of spherical aberration. With positive spherical aberration, the more highly curved peripheral portion of the lens focuses light in front of rays that pass centrally (top). With negative spherical aberration, peripheral rays are brought to focus behind the more central rays (middle). Photograph of an isolated dog lens through which parallel helium-neon laser beams have been passed (bottom). Beams that pass through the periphery of the lens are focused farther away from the lens than are beams that pass through the central portion of the lens, suggesting that dog lenses have negative spherical aberration. It has been postulated that this arrangement may compensate for positive spherical aberration of the peripheral portion of the canine cornea. (Photo courtesy of Dr. Jakob Sivak)

Spherical aberrations of the lens result in uneven bending of light rays across its convex optical surface (Fig 4). Positive spherical aberration occurs when light rays passing through the more highly curved periphery of the lens are brought into focus in front of the rays that pass more centrally. Many species of animals have compensated for this effect, and in these species, there is a gradient of refractive indices throughout the lens such that the more peripheral cortical fibers have a lesser refractive index (ie, a lesser ability to bend light) than do the more central fibers. Dogs actually have negative spherical aberration, and the peripheral rays are brought to focus behind the more central rays.[44] It has been suggested that negative spherical aberration of the lens in dogs may serve to compensate for positive spherical aberration of the peripheral portion of the cornea. The optics of the peripheral region of the cornea in dogs, however, remain to be investigated.

Figure 5—Photograph illustrating chromatic aberration. Red and green lasers have been superimposed and subsequently passed through an isolated lens of a fish. The shorter wavelength light (green) is focused in front of the longer wavelength light (red). (Photo courtesy of Dr. Jake Sivak)

Another common type of aberration in many vertebrate eyes is chromatic aberration, whereby light of short wavelengths (blue) is focused in front of light of long wavelengths (red; Fig 5). In a survey of the degree of chromatic aberration in vertebrates, it was found that most eyes had a relatively constant amount of chromatic aberration amounting to 4.6% of the equivalent focal length.[45] Surprisingly, dogs were found to have the greatest amount of chromatic aberration in this survey (5.7% of the equivalent focal length).[45] Although the clinical importance of chromatic aberration in dogs remains unclear, it was suggested that this high degree of chromatic aberration may reflect fundamental differences in the composition of the lens between dogs and the other species that were studied, in such factors as water content, protein distribution, or packing of lens fibers. Additionally, the relative insensitivity of canine cones to the longer (ie, red) wavelengths of light may minimize the impact of this aberration on visual performance.

Although visual acuity requires that the optical portions of the eye be transparent and that optical blur from refractive errors or astigmatism be limited, an adjustable focusing (accommodative) mechanism is also needed if objects at different distances are to be seen with equal clarity.[1] In dogs, accommodation may be brought about by altering the curvature of the lens surface or by moving the lens anteriorly, as has been demonstrated in raccoons.[46] Dogs generally have a limited accommodative range that does not exceed 2 to 3 diopters.[1,3] This suggests that dogs are capable of accurately imaging on the retina objects that are within 50 to 33 cm of their eyes, but that objects nearer than this will be blurred. Hence, dogs must use other senses, such as smell or taste, to augment vision in the investigation of very near objects. For comparison, young children are capable of accommodating approximately 14 diopters or to about 7 cm.[47] With age, the ability to accommodate declines (ie, presbyopia develops), perhaps as a result of increased resistance of the lens to changes in shape, or as a result of alterations in the excursions of the ciliary body musculature.[47] Loss of the lens, as occurs during cataract surgery, obviously creates a significant change in the refractive state of the eye.[38,48] The result is severe hyperopia (farsightedness), with objects being focused approximately 14 diopters behind infinity, and a reduction in visual acuity to 20/800 or worse.[43] This means that aphakic eyes are unable to image any object clearly, whether near or far away, and are unable to accommodate (Fig 6).[48] Although aphakic dogs are farsighted, it must be kept in mind that, for objects of similar size, objects that are closer to the dog will create a larger image on the retina than will objects that are located far away. Therefore, aphakic dogs may be able to better visually orient to near objects, despite being farsighted.

Figure 6—Simulation of the optical impact of 1 diopter of myopia and 14 diopters of hyperopia. A typical scene as it would appear to an individual with normal vision (top). The same scene with the camera focused at 1 meter, which simulates 1 diopter of myopia (middle). The same scene as it would appear to an individual with 14 diopters of hyperopia as occurs following lensectomy in dogs without optical correction (bottom). Notice that this illustration differs from true canine vision in regards to actual visual acuity, field of view, and the color spectrum perceived.

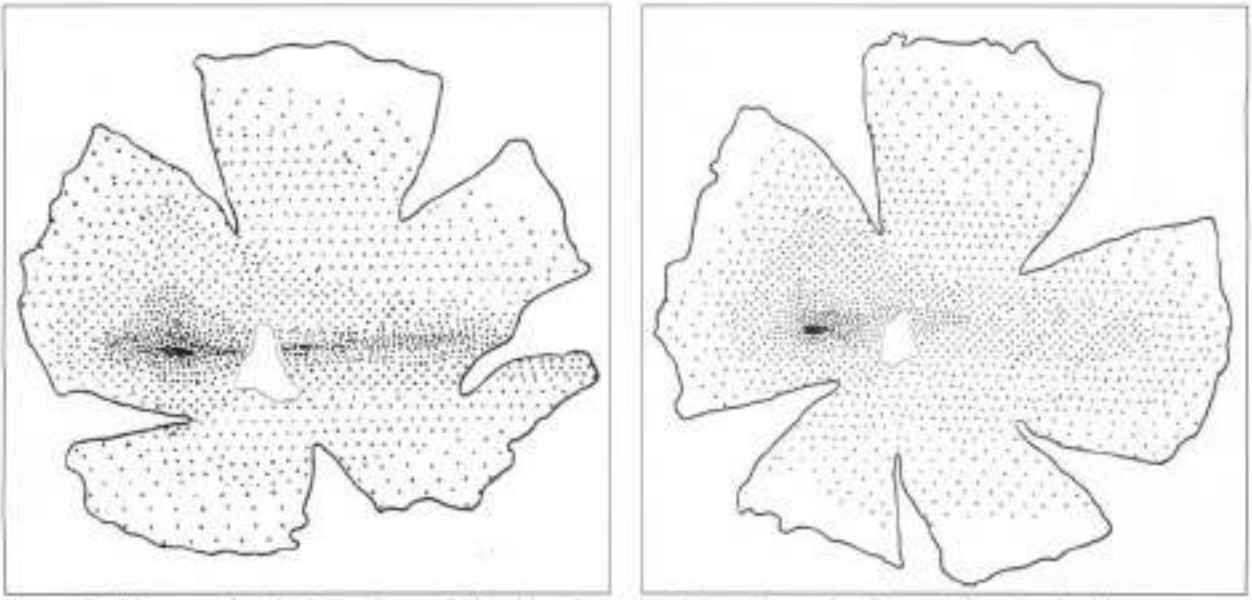

Figure 7—Diagram of retinal ganglion cell densities from the right retinas of a German Shepherd with a very pronounced wolf-like visual streak (left) and a Beagle with a moderately pronounced visual streak (right). Retinas were cut radially to flatten them and are displayed at the same magnification. The intensity of the dots reflects varying ganglion cell densities. The irregular shape in the center of each retina is the region of the optic nerve head. Ganglion cells could not be seen in this area because of thick, overlying nerve fiber layer. (Modified with permission from "The topography of ganglion cells in the dog and wolf retina" by Leo Peichl, *J Comp Neurol* 1992;324:603–620)

The degree of hyperopia associated with aphakia can be approximated for a human observer by setting a direct ophthalmoscope to −14 diopters and viewing the room through the view-port. Surprisingly, although this degree of hyperopia is markedly debilitating to some dogs, most dogs are still able to adequately orient themselves visually in their environment without correction. They would not, however, be able to perform visually challenging tasks. Because of the dominance of foveal vision in people, a similar loss of optical power is extremely debilitating and renders a patient functionally blind. Recently, corrective intraocular lenses have been designed specifically for use in dogs. These lenses are used in an effort to maximize visual recovery by restoring emmetropia following cataract removal.[48]

Retinal factors in visual acuity—The retina may be the limiting factor in visual acuity for normal dogs,[35] and its architecture may provide clues to the potential visual abilities of the canine eye. Enhanced vision in dim light, as occurs in dogs, typically necessitates that a greater number of photoreceptors (primarily rods) synaptically converge on a single ganglion cell. This tends to result in reduced visual acuity, however, just as high speed camera film produces a grainy image in bright daylight. On the other hand, retinas with excellent resolving power have a high ratio of ganglion cells:photoreceptors,[1] a large number of ganglion cells and optic nerve fibers, and a high density of photoreceptors. For example, the human optic nerve contains 1.2 million nerve fibers versus 167,000 in the canine optic nerve and 116,000 to 165,000 in that of cats.[49-53] In primates, the fovea has 1 ganglion cell per cone; in cats,[21] there are 4 cones for each ganglion cell in the retinal area capable of greatest resolution. Dogs are probably similar to cats, although the ratio of rods or cones to ganglion cells has not been determined for dogs. The size of a specific type of retinal ganglion cell, the beta/X cell, in the central portion of the retina limits the resolving power of the ganglion cell system, because it is the smallest ganglion cell with the smallest dendritic field.[21,54] These cells are critical in determining the *limits of visual* acuity and are approximately the same size in dogs and cats, suggesting that these 2 species potentially may have similar visual acuity.[54]

Dogs lack a fovea, which is found in people and other primates, but instead have a visual streak, which is the area of highest visual acuity.[30,55,56] The visual streak is oval and located superior and temporal to the optic nerve. It has short temporal and longer nasal extensions that are approximately linear (Fig 7).[30,55] In dogs, the visual streak is located in the tapetal portion of the retina, suggesting that vision in dim light may be enhanced, but that resolution of images in bright light may be degraded by scattered light.[55] The oval temporal part of the visual streak is generally free of blood vessels larger than capillaries (although some larger vessels may encroach into this area), and nerve fibers take a curved course to the optic disc dorsal and ventral to the visual streak, presumably to avoid reducing visual acuity in this region by interfering with light reaching the photoreceptors.[4,30,55] Detailed maps of visual pigment concentrations demonstrate that this area also has high concentrations of rhodopsin.[4] The oval temporal part of the visual streak also probably plays a role in enhancing binocular vision.[30,55] The nasal linear extension of the streak may facilitate scanning of the horizon, thereby allowing the dog to better use its wider field of view.[30,55]

There are fewer ganglion cells in the periphery of the retina than there are in the region of the visual streak. In monkeys, the ratio of cones:ganglion cells in

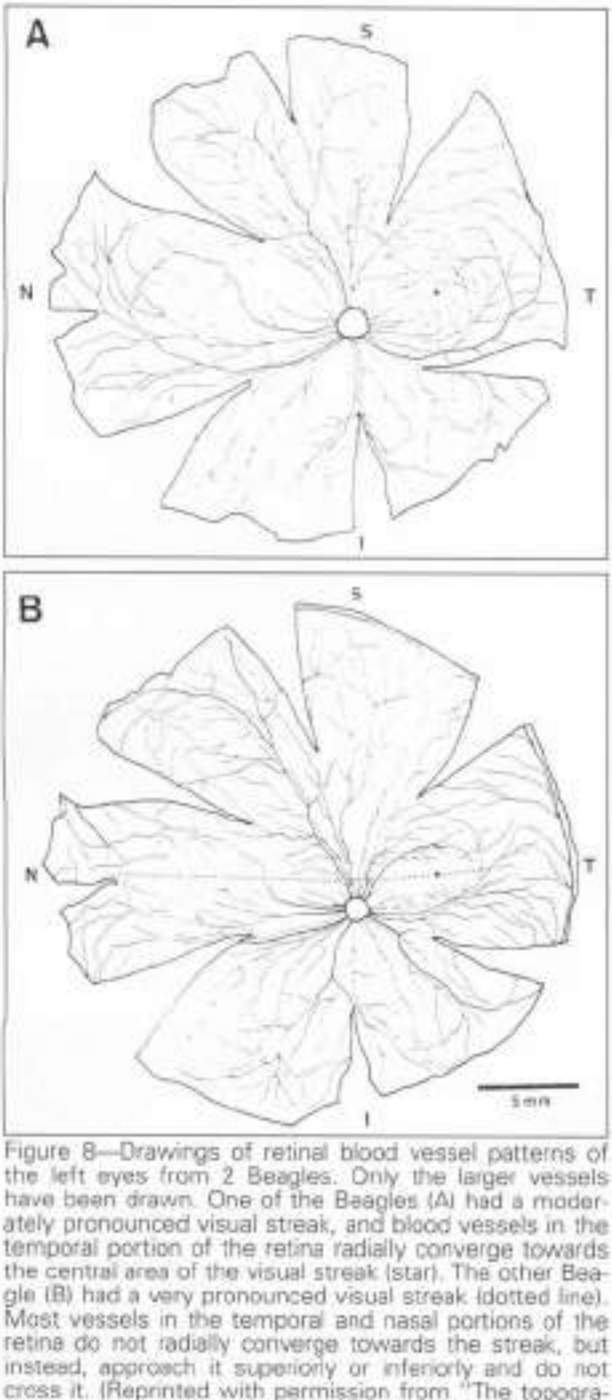

Figure 8—Drawings of retinal blood vessel patterns of the left eyes from 2 Beagles. Only the larger vessels have been drawn. One of the Beagles (A) had a moderately pronounced visual streak, and blood vessels in the temporal portion of the retina radially converge towards the central area of the visual streak (star). The other Beagle (B) had a very pronounced visual streak (dotted line). Most vessels in the temporal and nasal portions of the retina do not radially converge towards the streak, but instead, approach it superiorly or inferiorly and do not cross it. (Reprinted with permission from "The topography of ganglion cells in the dog and wolf retina" by Leo Peichl, *J Comp Neurol* 1992;324:603–620)

the fovea is 1:1, but at 10 mm eccentricity from the optical center of the retina, the ratio is 16:1. In cats, the ratio in the area centralis is 4:1 but increases to 20:1 in the peripheral portion of the retina.[21] Equivalent values for dogs could not be identified in the literature, but dogs probably are closer to cats than they are to monkeys. To compensate for reduced numbers of ganglion cells, the dendritic field size of the ganglion cells in the periphery *is increased*,[21] perhaps to permit increased sensitivity to light. Up to 20 different classes of ganglion cells may cover the mammalian retina,[21] suggesting that still poorly understood qualitative, as well as quantitative, differences in retinal function may exist in different regions of the retina.

Wolves, which presumably are the ancestral species of modern-day dogs, have a pronounced visual streak with a dense central area and extensions far into the temporal and nasal portions of the retina.[30] Such a streak may allow wolves to examine the visual horizon with relatively high visual acuity.[30] Domesticated dogs, in contrast, have been found to have either a pronounced visual streak, similar to that seen in wolves, or a smaller, less densely packed, moderately pronounced visual streak (Fig 7).[30,56] Wolves also generally have a greater maximum density of ganglion cells (12,000 to 14,000/mm^2) than do most dogs (6,400 to 14,400/mm^2).[30,56] This implies that the visual acuity in wolves may be better than that in dogs, and that the constancy of form of the visual streak in wolves may be a result of environmental pressures in their natural state. Similarly, the variation in appearance of the visual streak in domesticated dogs may be the result of breeding programs that place little selective pressure on maximizing visual performance.[30]

Different breeds of dogs have considerable differences in retinal ganglion cell topography (and therefore presumably in visual acuity),[30] and pronounced variations can also be found among individuals of a single breed. For instance, most of 1 strain of Beagles had a very pronounced streak, whereas most of another strain of Beagles had only a moderately pronounced streak.[30] Insufficient numbers of animals were studied to determine if differences exist between breeds that have been developed to hunt by sight (sight hounds) and breeds that have been developed to hunt by smell (scent hounds), although finding that a large number of Beagles (a scent hound) had a pronounced visual streak[30] would suggest that there may not be significant differences between these 2 groups of dogs, despite their uses. The pronounced and moderate forms of the visual streak may be differentiated during careful ophthalmoscopy of living dogs (Fig 8), although in the authors experience this is often very difficult to do with only a direct ophthalmoscope.[30] In dogs with a moderately pronounced visual streak, the retinal blood vessels covering the temporal portion of the retina converge towards the central area from all sides; in dogs with a very pronounced streak, the vessels approach the streak from the inferior and superior aspects of the retina and generally do not cross the streak.[30] Whether employing these criteria would aid in the selection of dogs with enhanced visual acuity, however, is still far from certain.

Estimates of visual acuity—The most familiar indicator of visual acuity in human beings is the Snellen fraction, which relates the ability of a subject to distinguish between letters or objects at a fixed distance (usually 20 feet or 6 meters) with a standard response. Snellen fractions of 20/20, 20/40, 20/100, for instance, mean that the test subject needs to be 20 feet away from a test image to discern the details that the average person with normal vision could resolve from 20, 40, or 100 feet away, respectively. For human beings, this test ac-

Table 1—Comparison of terms used to describe visual acuity. Derived from Borish[60]

Snellen value	Numerical value	Minutes of arc	Min/sec of arc	Cycles per degree
20/20	1.0	1.0	1′ 0″	30.0
20/25	0.80	1.25	1′ 15″	24.0
20/30	0.667	1.5	1′ 30″	20.0
20/35	0.571	1.75	1′ 45″	17.2
20/40	0.50	2.0	2′ 0″	15.0
20/45	0.444	2.25	2′ 15″	13.4
20/50	0.40	2.5	2′ 30″	12.0
20/55	0.364	2.75	2′ 45″	10.9
20/60	0.333	3.0	3′ 0″	10.0
20/65	0.308	3.25	3′ 15″	9.2
20/70	0.286	3.5	3′ 30″	8.6
20/75	0.267	3.75	3′ 45″	8.0
20/80	0.25	4.0	4′ 0″	7.5
20/85	0.235	4.25	4′ 15″	7.1
20/90	0.222	4.5	4′ 30″	6.7
20/95	0.21	4.75	4′ 45″	6.3
20/100	0.20	5.0	5′ 0″	6.0
20/150	0.133	7.5	7′ 30″	4.0
20/200	0.10	10.0	10′ 0″	3.0

tually measures the ability of the area of greatest visual acuity (ie, the fovea) to discriminate between objects. Peripheral visual acuity in people is typically poor (ie, 20/100, 20/200, or worse),[42] presumably because the photoreceptor density is lower and the ratio of photoreceptors to ganglion cells is higher in these regions of the retina than in the fovea.

Estimates of canine visual acuity vary widely, perhaps because they have been obtained by various methods, including behavioral testing,[57] measurement of visually evoked cortical potentials[35,43] or pattern electroretinography,[35,58] and assessment of the optokinetic response.[59] Each method has its own units for expressing visual acuity, although these units are comparable (Table 1).[60] One unit is the minimum angle of resolution, that is, the minimum distance by which 2 lines need to be separated to be distinguished as separate. This distance is typically expressed in minutes of arc of the visual field that separates the lines. Another method of determining visual acuity uses repeating patterns, such as alternating light and dark bars,[35] and expresses visual acuity in cycles of alternation per degree of visual field.[35]

In behavioral tests, the visual acuity at high light intensity (37 lux) of a medium-sized dog was 4 minutes 50 seconds of arc, or approximately 20/95 with the Snellen chart.[57] When estimated by means of visual evoked potentials (the electrical response generated in the brain when the retina is stimulated by illuminated patterns), the visual acuity of 2 dogs was determined to be 12.6 cycles/degree, or approximately 20/50, although this was determined by extrapolation and therefore has the potential to overestimate visual acuity.[35] With a more sophisticated sweep visual evoked potential procedure, the maximal visual acuity of 3 Beagles was determined to be 7.0 to 9.5 cycles/degree (20/85 to 20/65 on the Snellen chart).[43] When electrical response of the retina rather than response of the cerebral cortex was used, a mean threshold of 11.6 cycles/degree (approx 20/50) was obtained for 4 dogs.[35] Another study using pattern electroretinography estimated mean acuity of the central 15° of the canine retina to be 6.9 minutes of arc/phase (approx 20/140), and the mean acuity of the toroidal 15° of retina around this central area to be 11.8 minutes of arc/phase (approx 20/235).[58]

Testing the optokinetic reflex to determine visual acuity involves projecting a grating pattern of horizontally or vertically arranged bars of light and dark on a screen placed a fixed distance away from the eyes.[59] The bars are made to appear to move across the screen, inducing a nystagmus in the test animal. By determining the minimum distance separating the bars required to produce nystagmus, the threshold of visual acuity can be estimated.[59] Although this method has several limitations, 1 study using horizontally moving bars in dogs suggests that the visual acuity of the dog is approximately 5 minutes of arc or about 20/100.[59]

If one assumes from all these studies that visual acuity in the typical dog is about 20/75, then from 20 feet away, dogs could only begin to distinguish the details of an object that a person with normal vision could differentiate from 75 feet away (Fig 9). It should be pointed out that the most commonly used procedures to determine vision in dogs (eg, determination of menace responses by moving a hand across the dog's visual field or the ability to follow a moving cotton ball) are testing the motion sensitivity of virtually the entire retina, and positive responses are still present even though visual acuity may be worse than 20/400 (a person with visual acuity of 20/400 would be considered legally blind). It must be remembered, however, that visually distinguishing the fine details in objects is less important for a dog's lifestyle than it is for most people (even for working dogs), and the trade-off of improved vision in dim light versus less acute vision in bright light allows dogs to exploit an ecological niche inaccessible to us.

Form Perception

In general, few carefully controlled studies have been performed on the abilities of dogs to perceive shapes,[61] although form perception in dogs is reported to be good.[1] Pavlov found that conditioned reflexes that depended on discriminating a circle from an ellipse with semi-axes in a ratio of 8:9 could be developed in dogs.[1] Another study[61] found that dogs rapidly learned to discriminate between horizontal and vertical lines, but learned more slowly to differentiate between upright and inverted triangles. Once learned, however, these distinctions were found to be independent of the size of the object, and whether the figure was given as an outline or completely filled in.[61]

Color Vision

The ability of dogs to distinguish color has been the subject of several studies with often conflicting results.[62-65] Many early behavioral studies indicated either that dogs lacked color vision, or that if they could discriminate hue, it was without importance to dogs, and form and brightness were more important.[1,64,65] Many of these early studies, however, were poorly controlled and more recent, well controlled studies have clearly documented that dogs possess and use color vision.[5,64,65]

Color sensitive cones are found in the canine retina; therefore, there is, at least, an anatomic potential for color vision in dogs.[66] Studies using antibodies to cone outer segments indicate that, morphologically, there ap-

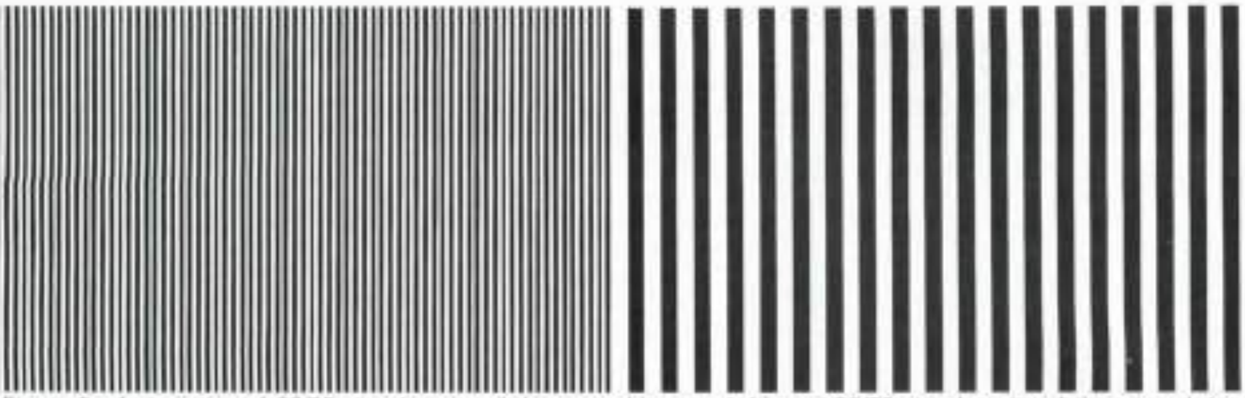

Figure 9—A depiction of 20/20 visual acuity of the normal human (left), and 20/75 visual acuity of the normal dog (right). The normal human with 20/20 vision can resolve the details of the fine lines on the right from 2 meters away, whereas the normal dog cannot. With visual acuity of 20/75, the human (and normal dog) can only resolve the lines on the left from the same distance.

pear to be 2 types of cones in dogs.[a] However, they comprise only a minority of the photoreceptors in the central area of the canine retina (probably < 10%), whereas in people, cones occupy virtually 100% of the central visual field's fovea.[67,68] Although 1 study[68] suggested that cones were slightly more concentrated in the central than in the peripheral portion of the retina in dogs, 2 other studies[4,67] have suggested that the distribution pattern is virtually uniform. Additional studies of the distribution of cones in the canine retina using more modern morphometric techniques are required before any definitive conclusions about regional variations in cone density can be made in dogs.

Behavioral discrimination testing and electroretinogram flicker photometry support the morphologic evidence for 2 types of canine cones.[5,65] One cone type is maximally sensitive to light with a wavelength of about 429 to 435 nm, which appears violet to people with normal color vision. The other type has a maximal sensitivity to light with a wavelength of about 555 nm, which appears yellow-green to people with normal color vision.[5,65] Although it is not known whether dogs perceive these 2 colors in the same way people do, it is suggested that the visible spectrum in dogs is divided into 2 hues: 1 in the violet and blue-violet range (430 to 475 nm wavelengths), which is probably seen as blue by dogs, and 1 in the greenish-yellow, yellow, and red range (500 to 620 nm wavelengths), which is probably seen as yellow by dogs (Fig 10).[65] Dogs probably also have a narrow region of the visible spectrum that appears colorless (a spectral neutral point). Light that ranges in wavelength from approximately 475 nm to 485 nm (blue-green to people) probably appears to be white or a shade of gray to dogs (Fig 10).[65] Wavelengths at the 2 ends of the spectrum (blue at 1 end and yellow at the other) probably provide the most saturated colors. Intermediate wavelengths are less intensely colored, appearing as if they were blends with white or gray. Therefore, in contrast to people, who are classically described as having trichromatic vision and see all wavelengths in the visible spectrum as hundreds of discriminable colors, the dog's color vision is dichromatic with a spectral neutral point.

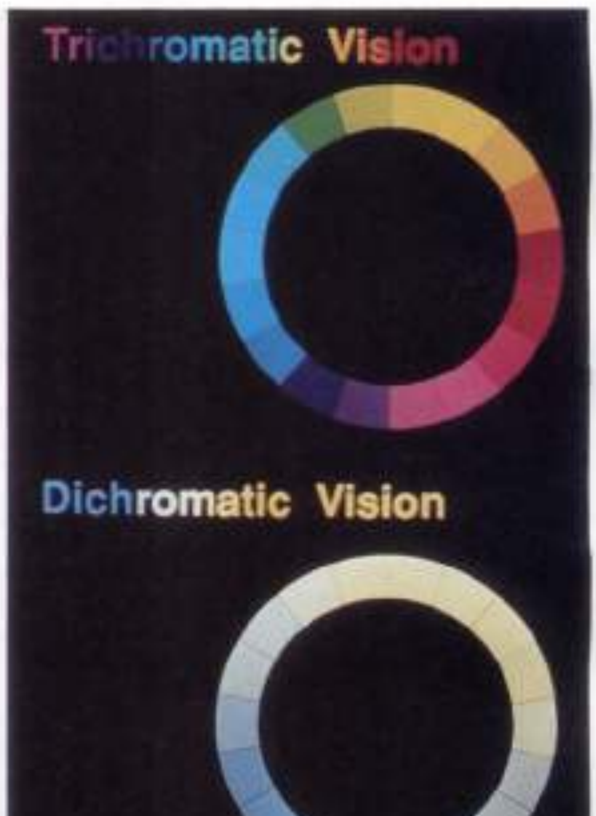

Figure 10—Comparison of the visible spectrum in individuals with trichromatic (top) or dichromatic (bottom) color vision. People with normal color vision are trichromatic; dogs are believed to be dichromatic. (Illustration courtesy of Dr. Jay Neitz)

Behavioral measures of wavelength discrimination have shown that dogs were able to differentiate wavelengths from about 440 to 520 nm (the region that includes what appears as violet, blue, blue-green, and green to people).[65] As stated previously, however, this does not mean that light in these wavelengths appears to be the same color to dogs and people. In fact, the appearances are probably different. The most striking differences in color vision between dogs and people is the dogs' inability to differentiate among middle to long wavelengths of light, which appear to people as green, yellow-green, yellow, orange, or red, and their inability to distinguish greenish-blue from gray. This pattern of color recognition is similar to that of a person with deuteranopia[65] (a type of dichromasy) who lacks cones sensitive to green light and characteristically tends to confuse red and green colors (red-green color blind). The dog differs, however, in that it has fewer cones, in general, than do human beings, and the colorless spectral neutral point in dogs is shifted toward the blue region of the spectrum (480 nm), whereas in people with deuteranopia, the spectral neutral point is in the green (505 nm) region of the spectrum. This difference in spectral neutral point may be the result of yellow pigment in the human lens that blocks short wavelength (blue) light and significantly reduces sensitivity to violet and blue light. Dogs lack such a yellow pigment in their lens.

Restrictions in color vision are probably of limited consequence in dogs, as it is likely that dogs react only to colors of biological importance to them.[54] Problems may arise, however, when people attempt to teach hunting and working dogs to distinguish among red, orange, yellow, and green objects solely on the basis of color. Additionally, a guide dog would be unable to differentiate among the signals at a stop light on the basis of color alone. In these cases, dogs must use clues other than color, such as smell, taste, texture, or other visual clues such as relative brightness and position, to differentiate between these similarly colored objects. On the other hand, Orbeli reported in 1909 that dogs are able to differentiate perfectly among closely related shades of gray that are indistinguishable to the human eye.[1] This ability would be a greater aid in increasing visual discrimination among animals adapted to function in low light levels than would enhanced color vision, because in low light conditions, there may be insufficient light to stimulate the cones.

Summary

Compared with the visual system in human beings, the canine visual system could be considered inferior in such aspects as degree of binocular overlap, color perception, accommodative range, and visual acuity. However, in other aspects of vision, such as ability to function in dim light, rapidity with which the retina can respond to another image (flicker fusion), field of view, ability to differentiate shades of gray, and, perhaps, ability to detect motion, the canine visual system probably surpasses the human visual system. This has made the dog a more efficient predator in certain environmental situations and permits it to exploit an ecological niche inaccessible to humans.

[a]Boden R, University of Berlin, Germany: Inaugural dissertation, 1909.

[b]Murphy CJ, School of Veterinary Medicine, University of Wisconsin, Madison, Wis: Unpublished data, 1993.

[c]Gropp K, Szel A, Aguirre G, James A Baker Institute for Animal Health, New York State College of Veterinary Medicine, Cornell University, Ithaca, NY: Personal communication, 1993.

References

1. Duke-Elder S. *System of ophthalmology. Vol 1. The eye in evolution.* St Louis: CV Mosby Co, 1958;605–706.
2. Walls GL. *The vertebrate eye and its adaptive radiation.* New York: Hafner Publishing Co, 1963.
3. Gunter R. The absolute threshold for vision in the cat. *J Physiol* 1951;114:8–15.
4. Kemp CM, Jacobson SG. Rhodopsin levels in the central retinas of normal miniature poodles and those with progressive rod-cone degeneration. *Exp Eye Res* 1992;54:947–956.
5. Jacobs GH, Deegan JF, Crognale MA, et al. Photopigments of dogs and foxes and their implications for canid vision. *Vis Neurosci* 1993;10:173–180.
6. Parkes JH, Aguirre G, Rockey JH, et al. Progressive rod-cone degeneration in the dog: characterization of the visual pigment. *Invest Ophthalmol Vis Sci* 1982;23:674–678.
7. Wen GY, Sturman JA, Shek JW. A comparative study of the tapetum, retina, and skull of the ferret, dog, and cat. *Lab Anim Sci* 1985;35:200–210.
8. Lesiuk TP, Braekevelt CR. Fine structure of the canine tapetum lucidum. *J Anat* 1983;136:157–164.
9. Burns MS, Bellhorn RW, Impellizzeri CW, et al. Development of hereditary tapetal degeneration in the beagle dog. *Curr Eye Res* 1988;7:103–114.
10. Weitzel G, Buddecke E, Fretzdorff AM, et al. Struktur der im tapetum lucidum von hund und fuchs enthaltenen zinkverbindung. *Z Physiol Chem* 1955;299:193–213.
11. Hebel R. Entwicklung und struktur der retina und des tapetum lucidum des hundes. *Ergeb Anat Entwicklungsgesch* 1971;45:3–92.
12. Wyman M, Donovan EF. The ocular fundus of the normal dog. *J Am Vet Med Assoc* 1965;147:17–26.
13. Murphy CJ, Pollock RVS. The eye. In: Evans HE, ed. *Miller's anatomy of the dog.* 3rd ed. Philadelphia: WB Saunders Co, 1993;1009–1057.
14. Rodieck RW. *The vertebrate retina: principles of structure and function.* San Francisco: WH Freeman Co, 1973;259.
15. Pirie A. Crystals of riboflavin making up the tapetum lucidum in the eye of the lemur. *Nature* 1959;183:985–986.
16. Elliot JH, Futterman S. Fluorescence in the tapetum of the cat's eye. *Arch Ophthalmol* 1963;70:531–534.
17. Pedler C. The fine structure of the tapetum cellulosum. *Exp Eye Res* 1963;2:189–195.
18. Coles JA. Some reflective properties of the tapetum lucidum of the cat's eye. *J Physiol (Lond)* 1971;212:393–409.
19. Leventhal AG, Creel DJ. Retinal projections and functional architecture of cortical areas 17 and 18 in the tyrosinase negative albino cat. *J Neurosci* 1985;5:795–807.
20. Rubin LF. *Inherited eye diseases in purebred dogs.* Baltimore: The Williams & Wilkins Co, 1989.
21. Wässle H, Boycott BB. Functional architecture of the mammalian retina. *Physiol Rev* 1991;71:447–480.
22. Aguirre G. Retinal degenerations in the dog. I. Rod dysplasia. *Exp Eye Res* 1978;26:233–253.
23. Aguirre GD, Rubin LF. The electroretinogram in dogs with inherited cone degeneration. *Invest Ophthalmol Vis Sci* 1975;14:840–847.
24. Dodt E, Wadensten L. The use of flicker electroretinography in the human eye: observations on some normal and pathological retinae. *Acta Ophthalmol* 1954;32:165–180.
25. Wadensten L. The use of flicker electroretinography in the human eye: observations on clinical cases. *Acta Ophthalmol* 1956;34:311–340.
26. Coile DC, Pollitz CH, Smith JC. Behavioral determination of critical flicker fusion in dogs. *Physiol Behav* 1989;45:1087–1092.
27. Hart WM. The temporal responsiveness of vision. In: Hart WM, ed. *Adler's physiology of the eye: clinical application.* 9th ed. St Louis: Mosby Year-Book Inc, 1992;548–578.

28. *The complete dog book.* 18th ed. New York: Howell Book House Inc, 1992.

29. Sherman SM, Wilson JR. Behavioral and morphological evidence for binocular competition in the postnatal development of the dog's visual system. *J Comp Neurol* 1975;161:183–195.

30. Peichl L. Topography of ganglion cells in the dog and wolf retina. *J Comp Neurol* 1992;324:603–620.

31. Bishop PO. Binocular vision. In: Moses RA, Hart WM, eds. *Adler's physiology of the eye: clinical application.* 8th ed. St Louis: CV Mosby Co, 1987;619–689.

32. Weale RA. *Focus on vision.* Cambridge: Harvard University Press, 1982;153–167.

33. Walk RD, Gibson EJ. A comparative and analytic study of visual depth perception. *Psychol Monogr* 1961;75:1–44.

34. Aguirre G, Rubin LF, Bistner SI. Development of the canine eye. *Am J Vet Res* 1972;33:2399–2414.

35. Odom JV, Bromberg NM, Dawson WW. Canine visual acuity: retinal and cortical field potentials evoked by pattern stimulation. *Am J Physiol* 1983;245:R637–R641.

36. Murphy CJ, Zadnik K, Mannis MJ. Myopia and refractive error in dogs. *Invest Ophthalmol Vis Sci* 1992;33:2459–2463.

37. Nowak MR, Neumann W. Refraktion des hundeauges. *Klin Monatsbl Augenheilkd* 1987;191:81–83.

38. Pollette L. Refraction of normal and aphakic canine eyes. *J Am Anim Hosp Assoc* 1982;18:323–326.

39. Worfeld BL. Canine optics. *Aust J Optom* 1965;48:164–174.

40. Dubar MJ, Thieulin MG. L'etat de refraction des yeux des mammiferes domestiques. *Rev Gen Med Vet* 1927;36:561–566.

41. Coile DC, O'Keefe LP. Schematic eyes for domestic animals. *Ophthalmic Physiol Opt* 1988;8:215–220.

42. Westheimer G. Visual Acuity. In: Hart WM, ed. *Adler's physiology of the eye: clinical application.* 9th ed. St Louis: Mosby Year-Book Inc, 1992;531–547.

43. Murphy CJ, Mutti DO, Zadnik K, et al. The effect of optical defocus on visual acuity in the dog. *Am J Vet Res* 1996; in press.

44. Sivak JG, Kreuzer RO. Spherical aberration of the crystalline lens. *Vision Res* 1983;23:59–70.

45. Kreuzer RO, Sivak JG. Chromatic aberration of the vertebrate lens. *Ophthalmic Physiol Opt* 1985;5:33–41.

46. Rohen JW, Kaufman PL, Eichhorn M, et al. Functional morphology of accommodation in the raccoon. *Exp Eye Res* 1989;48:523–537.

47. Kaufman P. Accommodation and presbyopia: neuromuscular and biophysical aspects. In: Hart WM, ed. *Adler's physiology of the eye: clinical application.* 9th ed. St Louis: Mosby Year-Book Inc, 1992;391–411.

48. Davidson MG, Murphy CJ, Nasisse MP, et al. Refractive state of aphakic and pseudophakic eyes of dogs. *Am J Vet Res* 1993;54:174–177.

49. Potts AM, Hodges D, Shelman CB, et al. Morphology of the primate optic nerve: method and total fiber count. *Invest Ophthalmol Vis Sci* 1972;11:980–988.

50. Arey LB, Gore M. The numerical relationship between the ganglion cells of the retina and the fibers in the optic nerve of the dog. *J Comp Neurol* 1942;76:609–617.

51. Stone J. The number and distribution of ganglion cells in the cat's retina. *J Comp Neurol* 1978;180:753–772.

52. Williams RW, Cavada C, Reinoso-Suárez F. Rapid evolution of the visual system: a cellular assay of the retina and dorsal lateral geniculate nucleus of the Spanish wildcat and the domestic cat. *J Neurosci* 1993;13:208–228.

53. Williams RW, Bastiani MJ, Lia B, et al. Growth cones, dying axons, and developmental fluctuations in the fiber population of the cat's optic nerve. *J Comp Neurol* 1986;246:32–69.

54. Peichl L. Morphological types of ganglion cells in the dog and wolf retina. *J Comp Neurol* 1992;324:590–602.

55. Hebel R. Distribution of retinal ganglion cells in 5 mammalian species (pig, sheep, ox, horse, dog). *Anat Embryol (Berl)* 1976;150:45–51.

56. Krinke A, Schnider K, Lundbeck E, et al. Ganglionic cell distribution in the central area of the beagle dog retina. *Zentralbl Veterinarmed C Anat Histol Embryol* 1981;10:26–35.

57. Neuhaus W, Regenfuss E. Uber die sehscharfe des haushundes bei verschiedenen helligkeiten. *Z Vgl Physiol* 1967;57:137–146.

58. Ofri R, Dawson WW, Gelatt KN. Visual resolution in normal and glaucomatous dogs determined by pattern electroretinogram. *Prog Vet Comp Ophthalmol* 1993;3:111–116.

59. Ezeh PI, Myers LJ, Cummins KA, et al. Utilizing an optokinetic device in assessing the functional visual acuity of the dog. *Prog Vet Neurol* 1990;1:427–432.

60. Borish IM. *Clinical refraction. Volume 1.* 3rd ed. Chicago: The Professional Press Inc, 1975;373.

61. Karn WH, Munn NL. Visual pattern discrimination in the dog. *J Genet Psychol* 1932;40:363–374.

62. Jacobs GH. The distribution and nature of color vision among the mammals. *Biol Rev* 1993;68:413–471.

63. Schmidt-Morand D. Vision in the animal kingdom. *Vet Int* 1992;1:3–32.

64. Rosengren A. Experiments in colour discrimination in dogs. *Acta Zool Fenn* 1969;121:1–19.

65. Neitz J, Geist T, Jacobs GH. Color vision in the dog. *Vis Neurosci* 1989;3:119–125.

66. Jacobs GH. Colour vision in animals. *Endeavour* 1983;7:137–140.

67. Parry HB. Degenerations of the dog retina I. Structure and development of the retina of the normal dog. *Br J Ophthalmol* 1953;37:385–404.

68. Koch SA, Rubin LF. Distribution of cones in retina of the normal dog. *Am J Vet Res* 1972;33:361–363.

Correction: Histologic appearance of axial osteochondral fragments from the proximoplantar/proximopalmar aspect of the proximal phalanx in horses

In "Histologic appearance of axial oesteochondral fragments from the proximoplantar/proximopalmar aspect of the proximal phalanx in horses" (*JAVMA*, Oct 15, 1995, pp 1076–1080), the last sentence beginning on page 1078, which ends at the top of page 1079, should read, "The position of these fragments between the base of the sesamoid bone and the plantar/palmar perimeter of the proximal phalanx suggests that lameness may have been a result of stretching of the synovial and fibrous attachments of these fragments to adjacent structures during full extension of the metatarsophalangeal/metacarpophalangeal joint." An extra phrase was inadvertently added to the sentence. The *JAVMA* regrets the error.