

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

Functional Performance of the Visual System in Dogs and Humans: A Comparative Perspective

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Vision in dogs is generally considered poor compared with humans, and recent reports have reviewed some of the physiological principles underpinning dog vision, but a systematic comparison of the physiological and neurobiological features of vision in dogs compared with humans appears to be lacking. This means there is a risk of an anthropocentric perspective of the topic rather than an understanding grounded in a wider biological context. It is also important to appreciate that deficits in one aspect may be compensated for in other parts of the visual system, so generalizing about performance on the basis of a single feature within the visual system might be misleading. This review provides an overview of the visual perceptual abilities of dogs versus humans, grounded in the visual system's physical structures (see supplementary information) for detecting different visual features of the environment through to its initial processing prior to its cognitive evaluation. Differences and variations that exist between dogs and humans and why these might occur are considered, by reference to their natural history (ecological factors affecting their evolution) and differences in morphology (including differences in height, which will affect viewpoint and the visual information available to individuals in the same location). The implications of differences and applications for everyday handling and training of the dogs are discussed throughout.

Keywords: *vision, visual functioning, dog, human*

General Introduction

Dogs and humans often work together, and dogs have been selectively bred for traits enabling efficient co-operation with humans, such as tameness (Miklósi, 2008), sensitivity to human cues (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Cooper et al., 2003; Virányi,

Topál, Gácsi, Miklósi, & Csányi, 2004), and specialized skills employed by specific types of working dog (Lord, Schneider, & Coppinger, 2016; McKinley & Sambrook, 2000; Miklósi, 2008). As a result, dogs are integral to society and have both important value (e.g., companion,

guide or assistant dogs) and economic value (Hall, Dolling, Bristow, Fuller, & Mills, 2016) to humans.

As running predators, dogs have vision that could be expected to be tuned to motion detection rather than visual acuity (McGreevy, Grassi, & Harman, 2004), but now some evidence suggests that dogs may use visual information more than wolves (Lord, 2013) and attend to the detail of human faces (Barber, Randi, Müller & Huber, 2016; Mongillo, Scandurra, Kramer, & Marinelli, 2017; Racca et al., 2010; Siniscalchi, d'Ingeo, & Quaranta, 2018; Somppi, Törnqvist, Kujala, Hänninen, Krause & Vainio, 2016), so there may have been selection for increased visual performance in dogs during domestication and breed diversification. Historical co-operation with humans and the wealth of visual cues and signals produced by humans are likely to make attention to visual information important to dogs if they wish to respond to human instruction and predict human behavior.

Breed diversification in dogs post domestication might also have diverse effects on vision depending on the function of the breed. For instance, a need for frequent social interactions with humans at close range might promote the development of higher visual acuity, whereas those engaged less directly or less visually (e.g., scent hounds) might not have been subject to the same selective pressures. However, in the literature such potential diversity is often, though not always (see Byosiere, Chouinard, Howell, & Bennett, 2018; Gácsi, McGreevy, Kara, & Miklósi, 2009; Georgevsky, Carrasco, Valenzuela, & McGreevy, 2014; McGreevy et al., 2013), ignored, and perceptual

research based on small sample sizes that likely do not reflect important breed variation are often generalized to all dogs. It is therefore important to appreciate not just average visual ability or the range of visual abilities but the factors that might be impacted by this—in particular, the differences in perception between dog breeds and the impact of correlated features such as early experience differences. In this regard it should not be assumed that differences in vision and also visual orientation toward humans associated with breed are necessarily genetic.

In this review we consider the various performance metrics of the visual systems of the two species, how this might vary between and within both species, and the implications of this variation. To support this, we provide a thorough review of the known anatomical variation that occurs in the visual system between humans and dogs in the supplementary information. Given differences in ecological function between dogs and humans, it is not surprising that there are large general differences in the functional performance of the visual systems, but as we have already highlighted there is also probably meaningful variation among dogs that should not be considered random noise, and readers are encouraged to reflect on its possible ecological significance and the practical implications of this. Indeed, even where such variation has not been established, we urge the reader to give consideration to the potential for this and its implications given the functional diversity of dogs. For those not familiar with the anatomy or physiology of vision, it may be useful to review some of the supplementary information first.

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Visual Perspective

From the outset, it must be recognized that dogs and humans tend to operate from different visual perspectives. Adult humans have an average height of 165–180 cm, and therefore their visual perspectives have little variation. However, dogs' shoulder heights vary from approximately 15 to 110 cm (The Kennel Club, 2018), therefore their vision is generally more closely oriented toward the ground than ours. However, this difference is especially pronounced in the small breeds. This is likely to have a substantial impact on perception between dog breeds (see Byosiere et al., 2018, for useful examples) but is also likely to result in a profound difference in experience between humans and dogs. This may vary from simply not perceiving a cue because of differences in perspective to substantial differences in

experience of the same situation. For example, when moving through crowds, most adult humans are able to visually orientate; however, even large dogs would have their vision obscured. This is likely to impact the animal in terms of both perception and emotion and may result in fearfulness. This consideration is important for pets who are frequently asked to walk streets among crowds in contexts from busy shopping street to parties and for working animals, as being in a crowd or crowd control may be part of their job.

Stereopsis

Stereopsis is important for depth perception and derives from binocular vision. It is limited by two factors: the position of the eyes (i.e., visual field and binocular overlap) and the amount of decussation at the chiasm (Herron, Martin, & Joyce, 1978). In the horizontal plane, humans with their frontally placed eyes have a visual field of $\sim 180^{\circ}$ – 190° (Sherman & Wilson, 1975; Wolfe, Kluender, & Levi, 2010) with a binocular overlap of 110° – 140° (Miller, 2001; Wolfe et al., 2010); vertically vision is restricted by the cheeks and eyebrows, and humans can see $\sim 60^{\circ}$ above and 80° below the center of gaze (Wolfe et al., 2010). In dogs, the size of the visual field is influenced by a variety of factors, such as eye position (frontal vs. lateral positioning), ear position (overhanging the lateral visual field), the nature of their fur covering (e.g., overhanging the eyes), and snout length. Consequently, the size of the horizontal visual field in dogs is very breed dependent and varies from 150° to 240° (Miller, 2001; Peichl, 1992; Sherman & Wilson, 1975) with a binocular overlap of 15° – 110° (Beaver, 1999; Miller, 2001; Sherman & Wilson, 1975).

This bigger horizontal visual field, especially for dogs with laterally placed eyes (paired with a retinal visual streak; for more information, see supplementary information), potentially provides them with a superior ability to scan the horizon compared with humans, which may have historically aided the hunting partnership. This ability in working dogs is likely to provide a substantial benefit to humans, as dogs will be able to anticipate challenges sooner, be it moving traffic in a guide dog or potential threats perceived by a protection animal. Although there are no existing data, dogs (especially dolichocephalic breeds, i.e., long-nosed dogs like greyhounds, Doberman pinschers, and poodles) have their vertical visual field blocked by the snout, and therefore seeing immediately below them is more restricted than in humans. This is likely to impact

their perception of unexpected changes in surface and may impact their ability to anticipate changes in terrain, particularly important in guide dogs and potentially search and rescue dogs working on difficult terrain. Furthermore, with laterally placed eyes, dolichocephalic breeds have less binocular overlap than brachycephalic breeds (i.e., short-nosed dogs like French bulldogs, pugs, and boxers) and so can be expected to have poorer depth perception. These differences should be considered when choosing dogs for tasks that may require accurate depth perception, including certain forms of search tasks and when navigating in challenging terrains. The differences in perception between dogs and humans are also likely to be important in respect to assistance dogs when making judgments about routes and moving traffic. Although it should be noted that these issues may, at least partially, be compensated for by training to increase proprioceptive awareness of limb position in search dogs.

Visual Acuity

Differences in eye composition (e.g., optical power of lenses, distribution of photoreceptors and ganglion cells in retina; see supplementary information) between dogs and humans result in differences in visual acuity between the two species. Among dogs, differences in the shape and composition of the area centralis are common; therefore it might be anticipated that brachycephalic breeds have better visual acuity, but reduced movement detection, compared with the dolichocephalic breeds, who may have better visual acuity along a horizon (McGreevy et al., 2004). Nonetheless, dogs have generally poorer visual acuity than humans; it is estimated to be typically 3 to 8 times worse than humans' (Lind, Milton, Andersson, Jensen, & Roth, 2017; Siniscalchi, d'Ingeo, Fornelli, & Quaranta, 2017), but this difference varies with light conditions: Dogs have been reported to be up to 15 times worse at resolving images than humans under bright light conditions; however, this ratio falls to 2.5 in lower light levels—those approximately equivalent to a full-moon night (Lind et al., 2017; Neuhaus & Regenfuss, 1967). A detailed list of existing data on the visual acuity in dogs and humans can be found in the supplements (Table S3). It does not seem that performance in light conditions lower than full-moon brightness equivalents or in a systematic way have been compared between the two species. Thus, for much of the spectrum where both species can see, humans are better able to discriminate detail, but as just mentioned (and discussed further

next), dogs appear better adapted than humans to see in lower light conditions. As a result, dogs are likely to miss specific detail, which is important to consider in their training. If pattern information is important for targeting, then they are likely to find that challenging to learn (van der Zee, Zulch, & Mills, 2012). However, dogs are likely to be better able to make important visual discriminations under lower light conditions. This might be particularly relevant in protection animals or search and rescue, as dogs may be able to perceive minor changes in their environment more readily than humans. This may be problematic, because sensitivity to small differences in surroundings may heighten responses to incidental changes, which humans cannot perceive but could, under certain conditions, result in sensitisation of the dog. It has been reported that humans need a brightness of at least 100 cd/m² for high visual acuity (Reidenbach, Dollinger, Ott, Janßen, & Brose, 2008). It is not known at what brightness dogs' acuity is best.

Another critical factor affecting visual acuity is the accommodation of the eye (the ability to focus an image on the retina). Differences in the accommodation capacity of the lens arising from the structure of the lens and the strength of the ciliary body, and nature of the cornea and composition of the retina all contribute to reduced visual acuity in dogs compared with humans (see supplementary information for full details). Traditionally, dogs have been considered to be generally myopic (near-sighted; Magrane, 1977), but more recent research suggests they are emmetropic (normal sighted) or nearly emmetropic (Cook, 2009; Ofri et al., 2012). It should be noted that some different dog breeds have genetic predispositions to be either myopic (e.g., German shepherds) or hyperopic (far-sighted, e.g., huskies; Black, Browning, Collins, & Phillips, 2008; Coile, 2007; Collins, Phillips, Bhana, & Dayton, 2004; Cook, 2009; Ofri et al., 2012; Williams, Kubai, Murphy, & Mutti, 2011). Inherited myopia in dogs might be caused by an irregularity in the vitreous chamber depth (Mutti, Zadnik, & Murphy, 1999). Of interest, animals in guide dog programs suffer less from these problems (ametropia), which might be the result of either extensive ophthalmic evaluation prior to breeding and selection or rejecting dogs with visual disturbances during the training process (Murphy, Zadnik, & Mannis, 1992).

Visual Adaptation and Recovery

An important visual function is the ability to adapt to conditions of differing brightness. This includes

abilities such as the level of light required to see anything and the time taken to see clearly when moving from bright to dark conditions or the reverse.

Sensitivity to Light Intensity/Brightness

Dogs are more sensitive to bright light than are humans. The minimum illumination to elicit an electroretinogram response (a diagnostic test used to measure electrical activity of retinal cells) is 5.34×10^{-4} lm/m² for dogs (Schmidt, 1968), a threshold that may be around 1,000 times lower than in humans (Neuhaus & Regenfuss, 1967). Dogs have a number of adaptations that enhance their sensitivity to light: larger pupils and lenses (Wolfe et al., 2010), a tapetum lucidum (Schmidt, 1968), a rod-dominated retina, a rhodopsin peak sensitivity of 510 nm (Van Buren, 1964), and a greater Purkinje shift (Hrachovina, 1967; Miller & Murphy, 1995; Schmidt, 1968; see supplementary information for full details). However, this comes at a cost to photopic visual performance. When exposed to bright light, rhodopsin within rods is bleached out quickly because of an overconsumption of rhodopsin molecules (Minke, 1987) and the pigments in cones “take over” the supply of visual information to the brain (light adaptation). Compared with rods, cones are less sensitive to light and regenerate faster. Humans have more cones than dogs and are therefore better adapted to function optimally in bright light conditions. They are also better able to discriminate subtle brightness differences with a Weber fraction (relative difference threshold) of 0.1 in humans in contrast to 0.2–0.7 in dogs (Pretterer, Bubna-Littitz, Windischbauer, Gabler, & Griebel, 2004). How these differences translate to performance in real-world settings does not appear to have been evaluated and is perhaps a significant gap in our knowledge (i.e., to what extent humans can depend on dogs, or the converse, when their vision is compromised by lighting conditions). This sensitivity to brightness may impact animal welfare in areas where they are exposed to bright sunlight, particularly, for example, under desert warfare conditions and rescue services in snowy conditions, but also in urban environments with bright surfaces (e.g., light-colored pavings). It may also impact animals working performance under conditions with bright flashing lights, such as emergency service lights or in the theatre of war.

Dark Adaptation

Dark adaptation is of particular relevance, especially for service as well as police and military working dogs, because dogs may adapt at a very different rate to humans

when they shift from a bright to a dark environment, which is likely to impact performance under changes in lighting conditions. Initial dark adaptation involves a shift from cone-dominated photopic vision to rod-dominated scotopic vision, which takes ~5 min in humans and ~10 min in dogs (Schmidt, 1968). However, depending on the preceding light levels, rods need a variable amount of time to fully recover after extensive photoreceptor bleaching. This regeneration can take up to 70 min in dogs (Kemp & Jacobson, 1992) but is thought to take only 20–30 min in humans (Lamb & Pugh, 2004; Minke, 1987; Reidenbach et al., 2008). Previous research on cats suggests this slower regeneration process might be due to lower concentrations of 11-cis retinal molecules in retinal epithelium that are important for rhodopsin regeneration (Lamb & Pugh, 2004). Whether the same applies to dogs, or if there are differences between dog breeds, is unknown.

The shift from cone- to rod-dominated vision is affected by several factors. The first is the illumination level: The rod-cone shift occurs at much brighter levels in dogs at 60 cd/m² compared with 0.1 cd/m² in humans (Coile, Pollitz, & Smith, 1989), with full dark adaptation potentially occurring below 10⁻⁵ cd/m² in humans (Reidenbach et al., 2008) and 2.8 × 10⁻³ cd/m² in dogs, respectively (Schmidt, 1968).¹ The second factor is light intensity and exposure time during the preadaptation period: Following very bright or prolonged bright exposure, onset and completion of dark adaptation can be delayed as it takes photoreceptors longer to regenerate (Dressler, 1913; Reidenbach et al., 2008).

The third factor is wavelength: The wavelength of the light in the preadaptation period can affect adaptation speed. Rods are sensitive to short but not long wavelengths (see supplementary Figure S3), meaning they are rapidly bleached by short wavelengths that correspond to their peak sensitivity but more resistant to wavelengths on either side of this. In humans (e.g., in astronomical, aeronautical,

medical, or military settings), exposure to long wavelengths (e.g., red light) before entering dark environments helps to maintain visual function and accelerate dark adaptation (Eisenberg, 1995; Watson & Gorski, 2011), and it is predicted that a similar phenomenon would occur in dogs, albeit with a slightly different spectrum. Elucidating what these spectra may be and the impact that this may have on adaptation could have important implications for dogs working under these environmental conditions.

The fourth factor is age: In humans, the cone-rod shift is quicker in younger individuals (Dressler, 1913), and brightness sensitivity during scotopic vision reduces with aging (increasing the occurrence of night blindness; Reidenbach et al., 2008), but to date it seems there has been no research into the effect of age in dogs on this phenomenon.

The final factor is nutrition: Dark adaptation and scotopic vision performance require the consumption of vitamin A and anthocyanins in humans (Cideciyan, Pugh, Lamb, Huang, & Jacobson, 1977; Ghosh & Konishi, 2007). In dogs, antioxidant supplementation has beneficial effects on their visual functioning (Wang, Hernandez, Moore, Jackson, & Narfström, 2016), but whether vitamin A and anthocyanins might also benefit the process of dark adaptation is unknown.

Thus, at a practical level it should be expected that dogs may take longer than humans to adapt to dark environments after exposure to bright lighting, despite their better low-level vision; however, a number of potential strategies might mitigate against this, and looking at ways of optimizing this process may have important implications for dogs working in search environments with high contrast (e.g., caves, nighttime checkpoints).

Light Adaptation and Dazzling

In contrast to dark adaptation, light adaptation (shift from scotopic to photopic vision) is normally a fast process, taking ~50–100 ms in humans and accompanied by a sudden constriction of the pupil (pupillary light reflex), but its completion can take up to 10 min for full visual acuity and color vision to be restored (Reidenbach et al., 2008). In humans, light adaptation is dependent on similar factors to dark adaptation, such as operating illumination levels (full light adaptation occurring at brightness above 10 cd/m²), light intensity and exposure time during the preadaptation phase (the greater the preadaptation to dark, the slower the shift to photopic vision), wavelength (the more blueish the light, the faster the shift) and age (with aging resulting in decreased sensitivity to luminance but not

¹ Please note that this threshold is the luminance intensity used to directly stimulate retina photoreceptors, not the environmental ambient light. With the tapetum in a dog's eye, the ambient light level needed for the rod-cone break could be much lower. Furthermore, the rod-cone break just indicates that rods become more sensitive than cones at the cellular level at this intensity. In other words, we can say at the cellular level, dog rods will be more active than cones at a brighter environment in comparison with humans. It is unclear how this sensitivity difference at cellular level could be manifested at the visual perception or behavioral level between two species. Further research could explicitly address this question.

as dramatically as in scotopic vision; Reidenbach et al., 2008). It seems that light adaptation has not been researched in dogs. However, breed-related differences in dog retinal topography (e.g., horizontally aligned visual-streak in dolichocephalic breeds vs. a more pronounced area centralis in brachycephalic breeds) would lead us to predict different sensitivities to brightness. This should be considered when selecting dogs for tasks associated with sudden changes in light levels, such as building searches or warfare.

An individual can be dazzled by a sudden shift from a dark to a bright environment. Under this condition, cones have not started working, but all rods are instantaneously bleached out; the photoreceptor system generates a flood of neuronal signals, resulting in perceptual glaring (dazzling). Dazzling can cause discomfort and harm and can result in a temporary or even permanent blindness if exposure time is too long. Some guideline values for humans are given in the supplement in Table S4. In humans, luminance below 730 cd/m² is acceptable and does not cause glare, but dazzling is likely to be experienced (especially for a dark-adapted eye) beyond this threshold, though the eye is still able to adapt so long as luminance does not exceed 10⁴ cd/m². Levels greater than this result in a risk of eye damage (Reidenbach et al., 2008). It can be assumed that for the dark-adapted eye, the perceived strength of the glare will depend on the wavelength of the stimulating light, with shorter visible wavelengths creating more risk of dazzle (e.g., xenon vs halogen headlights; Reidenbach et al., 2008). These shorter wavelengths also appear to trigger stronger photoreceptive reactions in cats (Hrachovina, 1967); however, to our knowledge, the response and critical thresholds have not been investigated in dogs. From a theoretical perspective, the fact that rods dominate the dog retina alongside the physiological similarities would suggest that dogs may perceive a stronger and longer dazzling effect than humans, with a greater risk of damage.

Following glare or extensive exposure to bright light sources, humans will suffer from afterimages as a result of overstimulation of photoreceptors, which prolongs photochemical activity after the bright stimulus has vanished (Reidenbach et al., 2008). Afterimages can occur for several milliseconds to seconds, depending on preceding conditions, and interfere with visual performance. It is unclear whether dogs also perceive afterimages.

Regardless, the aftereffects of exposure to bright lights is an area that deserves further investigation, as it might be relevant to the capabilities of patrol dogs, especially because it is thought that high levels of visual

stimulation may also interfere with the functioning of the other senses. Anecdotally, dogs, like many other species, may show behavioral and physiological responses upon being dazzled, such as having the photic sneeze reflex, experiencing increased tear production, blinking, turning the head away from the glare, or even freezing, which may interfere with their functional performance. These may be important signs for handlers to be aware of.

Dazzling can also be caused by scattered light within the eye, which is more likely in aged eyes and in those with lighter irises. In the absence of data to the contrary, it is perhaps best to avoid the use of old dogs and dogs with this sort of iris when they are required to operate in bright or frequently contrasting light conditions.

Shifting Between Light Conditions

In humans, if an individual frequently shifts between bright and dark environments, the visual system will quickly fatigue and decrease its sensitivity, resulting in an increased latency to adapt (Reidenbach et al., 2008). This can lead to reduced functioning in a range of capacities (visual acuity, contrast sensitivity) in both photopic and scotopic vision. A similar effect can occur if an individual is exposed to a bright stimulus in an even brighter environment (e.g., computer monitor in front of a bright window; transient adaptation factor; Reidenbach et al., 2008). Given the similarities between the dog and human visual system, it should be presumed that dogs will experience similar visual fatigue under similar environmental conditions. As such and unless specified otherwise, we should not expect dogs to be able to perform under these conditions if they are challenging for us as humans.

Temporal Resolution of Light Stimuli

There is a maximum number of stimuli that can be processed in a given time interval (i.e., rate of updates of the retinal image), and this is referred to as the critical flicker fusion frequency threshold (CFF). Visual stimuli presented below the CFF will be perceived as flickering, and those above it will be perceived as steady. The CFF is related to the ecological niche of a species, with higher CFF observed in fast-moving animals, and is correlated with the density of rods in the retina but is also dependent on environmental illumination conditions. In a cone-dominated bright environment, CFF is ~70–80 Hz in dogs and ~50–60 Hz in humans (although some people can resolve up to 70 Hz; Coile et al., 1989; Payne, DeAraugo, Bennett, & McGreevy, 2016; Schmidt, 1968), whereas in a rod-dominated dim-light environment, CFF is ~20 Hz

in both dogs and humans (Miller & Murphy, 1995). The higher CFF in dogs in light conditions might explain why some dogs are not interested in television, which potentially has implications for the type of stimuli that “catch the attention” of individuals. Certain forms of lighting (especially fluorescent lighting) might produce a flicker for dogs that is not perceived by humans and may thus be a greater distraction to them; in humans, this can increase the risk of headaches. Whether a similar phenomenon occurs in dogs is unknown, but anecdotally, some pet dogs do appear to avoid some areas with fluorescent lighting. Flickering lights can also affect human mood and arousal levels by increasing visual imagery (Von Gizycki et al., 1998); a similar effect has been reported in cats (Kaneko, Hidaka, Hishikawa, Shimizu, & Miyazaki, 1961) and may therefore also occur in dogs, although there is no direct evidence of this. The potential aversiveness of flickering light depends on the brightness of the stimulus, illumination area and flickering frequency. In humans, flickering light is perceived as more bright compared with steady lights (Broca-Sulzner effect) in a wide range of circumstances (Halstead, 1941; Reidenbach et al., 2008; White, Belinda Collins, & Rinalducci, 1976) and prolonged exposure to high illumination flickering lights at 5–10 Hz can cause nausea, disorientation, and vertigo (Bucha effect; Bunker, 1997), as light at these frequencies interferes with brain waves associated with relaxation and sleep. Helicopter pilots can potentially suffer from the Bucha effect (at higher 24–27 Hz frequencies) as the rotor blades strobe the sunlight (Cushman & Floccare, 2007), but it is unclear whether dogs can suffer from this sort of effect. Nonetheless, the potential impact from the risk of this effect indicates that it should perhaps receive scientific attention.

Color Vision

Humans are trichromats and can differentiate hues of blue (380–550 nm), green (430–670 nm), and red (500–760 nm), whereas dogs are dichromats and can differentiate well only hues of blue (430–485 nm) and yellow (500–620 nm; Jacobs, Deegan, Crognale, & Fenwick, 1993; Miller & Murphy, 1995; Neitz, Geist, & Jacobs, 1989; Siniscalchi et al., 2017). Therefore, color vision in dogs resembles red–green color blindness in humans, but contrary to popular belief dogs can still discriminate red and green from gray; both dogs and humans have a spectral neutral point at 480 and 505 nm, respectively, which is important for differentiating shades of gray (Byosiere, Chouinard, Howell, & Bennett,

2019; Tanaka & Watanabe, 2000). Even though dogs see a narrower range of colors than humans, they tend to use color as a more important visual cue for differentiation than brightness differences (Kasparson, Badridze, & Maximov, 2013). However, color discrimination is strongly influenced by luminance levels (Byosiere et al., 2019). The limitations of dogs’ color vision have implications for training, especially the criteria to be used for selection of discriminatory stimuli. It is also important to consider during physical challenges for the dogs. For example, steps under certain color conditions may be challenging for a dog to perceive, resulting in their refusing to use the steps or, potentially, injuring themselves. The same is true of search or rescue missions, in which the target and background has certain color conditions that are difficult for the dog to discriminate, resulting in lowered success rates during training or, more crucially, in the field. Further, in cases where light is used for directing behavior, appropriate wavelengths should be chosen (e.g., blue and yellow light/lasers over green and red). This is an important consideration for both pet and working dogs. Equally, given that dogs have a greater number of S-cones across the retina than humans, they are likely to be more sensitive to blueish hues than we are. It is therefore possible that they might use this visual cue for discriminating between objects that appear identical in color to us. This is likely important when, as humans, we are anticipating their using another sensory modality. Indirect evidence for the predominance of the blue hue in dogs comes from the finding that dogs lenses are UV-transparent (Douglas & Jeffery, 2014). This, in combination with S-cones sensitivity to parts of the UV spectrum, suggests that UV light appears to dogs as a blue/violet hue. For further reading, see the supplementary information.

Human color vision declines with aging (Roy, Podgor, Collier, & Gunkel, 2004), but it is unclear whether aging affects dog color vision in a similar way (or at a similar rate), given that some of the changes associated with this decline in performance, such as accumulation of yellow pigments in the lens, do not seem to occur in dogs.

For many species, color perception plays an important moderating role in physiological and psychological processes. It can influence physiology (e.g., heart rate), sleep, mood, and cognitive functioning in humans (Knez, 2001; Kombeiz & Steidle, 2018; Lasauskaite & Cajochen, 2018; Noguchi & Sakaguchi, 1999; Scholkmann, Hafner, Metz, Wolf, & Wolf, 2017); in mice, those kept in a red cage were more anxious than

those kept in green, black, or white cages (Sherwin & Glen, 2003). The effect of accommodation color scheme on the mood of dogs remains unknown but may be of importance for optimizing their potential. It could allow working dogs to be kept in kennels of appropriate colors or transported in vehicle interior of certain colors. It may also allow pet owners to decorate the rooms in their home with colors that are more suitable for dogs.

Perception of Physical Features

Depth Perception

Depth perception is important for calculating the position and distance of objects in the environment. Many monocular cues can contribute to such calculations of distance, such as the relative size of an object (i.e., smaller when farther away), perspective (i.e., parallel lines converge with distance), and luminance (i.e., objects have lower luminance and color saturation when far away). Environmental factors, such as shadows of an object in relation to the background and light source, can also provide information to calculate the distance and size of an object. Another important cue is the change in object characteristics during movement (i.e., the relative movement of an object against the background) with nearby objects appearing faster than faraway objects. Although the ability to accurately judge distance using these cues depends partly on experience, cues from the oculomotor system itself can also provide distance information because of feedback loops between the brain and the muscles of the lens (Wolfe et al., 2010). However, depth perception is more accurate and efficient with binocular vision. The disparity of the retinal images enables the brain to triangulate the position and distance of an object with high accuracy. Although it may be thought that this capacity is particularly important for hunting, this may not be the case, and it is worth noting that most sight hounds (a traditional type of hunting dog) have relatively laterally placed eyes with little binocular vision. As already discussed, the extent of the binocular visual field varies greatly between dog breeds (15° – 110°) depending on the positioning of their eyes. Thus, for hunting the exact distance may be of little importance except for the kill, when other cues, such as tactile feedback around the mouth, may be more valuable. Depth perception abilities, however, may be important to certain forms of working dog; for example, a guide dog should be able to accurately determine distance to the curb or other objects to guide and protect its handler, and working dogs used in difficult terrains such

as mountains should be able to reliably judge distances when negotiating gaps. It is essential that we are aware of these differences to allow us to train animals in a way that allows them to perform the job they are asked to do and to ensure maximum welfare for these working dogs.

Puppies have good monocular and binocular depth perception (Walk & Gibson, 1961) but can be expected to improve as the animal and its visual system matures with relevant exposure (Miller & Murphy, 1995). It is unclear how poor depth perception is in dogs' peripheral visual field because of the alpha-cell gap (Peichl, Ott, & Boycott, 1987; for further reading, see supplementary reading; Miller & Murphy).

Motion Detection

The detection of movement is biologically important (e.g., for detecting possible prey or predators). Movement and/or motion-induced changes in the features of an object, such as changes in size or shape, may make it easier to detect moving objects over static ones. For instance, German shepherds can detect a moving target up to 800–900 m away but a stationary object up to 585 m away (Miller & Murphy, 1995). At a practical level, training to detect a moving target may aid the later ability to detect the same target when static.

It is possible to perceive motion with a static retinal image, if the eyes or head track the moving target. In this case, the eye and head movements serve as a reference to calculate the movement of the target (e.g., speed; Wolfe et al., 2010). During motion detection within the eye, the visual system detects changes in luminance along the retina. This information is subsequently compared and aligned to that provided by neighboring retinal photoreceptors; rods are especially important in this regard (see supplementary information). In humans, rods are concentrated in the peripheral retina, leading to superior motion detection capability in the peripheral visual field (especially) in scotopic and mesoscopic conditions (Van De Grind, Koenderink, & Van Doorn, 2000; Williamson & Cummins, 1983); the threshold for motion detection is also linearly related to visual acuity (Van De Grind et al., 2000). In dogs, rods are widely distributed over the whole retina, suggesting that they may be more sensitive to motion detection in scotopic and mesoscopic conditions than humans; however, the alpha-ganglion cell gap in their temporal retina might limit their peripheral movement sensitivity. Breed-related differences in retinal composition (see supplementary information) might also lead to differing motion detection sensitivities. Still, dogs are likely to be better

able to perceive movement under certain conditions compared with humans, and this might be particularly relevant in protection or search and rescue animals, as the dogs may perceive aspects of the environment that humans are unable to perceive.

In humans, motion signals are also processed by specific “motion sensors” at different stages of the visual pathway; this includes motion-sensitive retinal ganglion cells and lateral geniculate nucleus (LGN) neurons, as well as direction selective neurons in area V1 and the middle temporal lobe of humans (for a review, see Kolb & Whishaw, 2014; Wolfe et al., 2010), but the neural mechanism underpinning motion perception in dogs is less clear. For further reading on the neuronal basis of vision, see the supplementary information.

Common motion cues involved in perception include apparent motion, coherent motion and biological motion. Apparent motion is the visual illusion that forms the basis of movies: it is the product of a series of static images displayed in a consecutive order at a certain speed, which are then perceived as smooth motion given the spatio-temporal integration of the successive stimuli (for further reading, see supplementary information). Coherent motion is the global representation of a moving pattern by integrating multiple local motion cues (Kolb & Whishaw, 2014; Wolfe et al., 2010). A recent study in dogs suggests that they are also sensitive to coherent motion, but at a lower level than humans, suggesting that dogs, at least under these conditions, are poorer at motion detection than humans. However, it should be noted that this is an artificial task and the differences observed may reflect other factors (Kanizsár et al., 2018; Kanizsár, Mongillo, Battaglini, Campana, & Marinelli, 2017).

Biological motion is the perception of animal/human movement by integrating a few local bodily motion cues (e.g., a few points representing major areas of joints movement), which is important for inferring and recognizing the action of another being (e.g., walking, running), its identity, intention, and possibly emotional state. Both humans and dogs are able to identify biological motion (Grossman & Blake, 1999; Ishikawa, Mills, Willmott, Mullineaux, & Guo, 2018). Of interest, after comparison, dogs paid more attention to human biological motion in the frontal view compared with dog biological motion, and their preference for biological motion in different viewing perspectives (frontal vs. lateral view) is modified by their sociability (Ishikawa et al., 2018). This, in combination with their greater sensitivity to motion under certain conditions, may result in dogs more readily detecting human motion in a potential search.

Similar to brightness- and color-induced visual after-effects, extensive exposure to motion stimuli can lead to a motion after-effect that may result from fatigue of the visual system, for example, looking intently at a waterfall and then shifting gaze to a static stone next to the waterfall results in the stone appearing to move in the opposite direction of the waterfall (waterfall illusion). In humans, such motion after-effects normally last less than 1 min, but in some cases they can last for days or even weeks (Anstis, Verstraten, & Mather, 1998); it is unclear whether dogs are subject to such after-effects, but it would be worth testing experimentally as well as determining whether there is any anecdotal evidence of this from handlers in the field. For example, dogs transported in fast-moving vehicles on a regular basis, might express a motion after-effect in the form of erratic behavior toward a stationary object once they are removed from the vehicle. If there is evidence of this sort of effect, then it may be advisable to transport animals with an opaque window, and the relevance of this to fieldwork would need careful consideration, especially if the effect is prolonged.

Size Perception

Accurate estimation of an object’s size (e.g., the body size of a predator or prey) is highly biologically relevant. The capacity for size perception is dependent partly on visual acuity (i.e., individuals with higher visual acuity will be more able to make accurate size discriminations), so humans might be expected to outperform dogs. However, size is clearly important to dogs, and in the labeling of objects they appear to have a size bias, whereas humans have a shape bias (van der Zee et al., 2012), that is, dogs preferentially use size over shape or texture to group objects by label. This may result in surprising differences in generalization between dogs and humans. If dogs are trained to respond to specific visual targets (e.g., to approach a car), they may use size rather than shape for this discrimination and thus approach objects of similar sizes rather than objects of similar shapes as a human would. Still, size discrimination and generalization processes have been neglected in recent research, even though these abilities are crucial especially for working dogs; as such, it is important to train for the specifics of the discrimination that we want dogs to make. Additionally, in a social context, both humans and dogs integrate cross-modal sensory information (e.g., auditory and visual information) to assess the size of another individual; that is, upon hearing a growl they can infer the size of

the sender (Bálint, Faragó, Dóka, Miklósi, & Pongrácz, 2013; Faragó et al., 2010; Taylor, Reby, & McComb, 2010, 2011) or other features such as the gender of a person (Ratcliffe, McComb, & Reby, 2014).

Visual perception of size is also dependent on the movement, luminance, distance, and retinal image position of the object, as well as the ability to integrate these cues in three-dimensional space. The ability to discriminate size is affected by age (Milgram, 2003; Milgram et al., 2000; Tapp et al., 2004). Dogs can reliably discriminate objects that differ in size by about 20%, which is comparable to data from humans and apes (Byosiere et al., 2018). When presented with a forced-choice task, they are more successful if they can choose the bigger object over the small one (Byosiere et al., 2018; but see also Tapp et al., 2004). Other visual cues such as color and shading may interfere with size cues and affect learning of a discrimination as a result (Milgram et al., 2000). There may also be sex differences in sensitivity to size cues, with one study finding that only females responded to an object suddenly appearing to be bigger or smaller after temporarily disappearing (Mueller, Mayer, Dorrenberg, Huber, & Range, 2011). This again suggests that subtle differences in perception need to be taken into account when asking animals to make important discriminations in the field.

Form Perception

In humans, form perception (i.e., the detection and recognition of patterns, shapes, or other salient features) occurs centrally in the hierarchical processes of the ventral visual pathway (visual cortical area V1 → V2 → V4 → inferior temporal cortex; for more details, see supplementary information). V1 neurons selectively encode basic form features, such as contrast, wavelength, and orientation; these basic features are later combined into components, such as edges and corners, in V2. They are further integrated into information about the form, such as contour and shape, in V4, and the inferior temporal cortex object perception and recognition is realized (Wolfe et al., 2010). The neuronal pathway of detection and recognition in dogs still needs clarification, but there is research to indicate that dogs can learn to discriminate between different objects varying in shape, size, distance, texture, brightness, color, or shading (Bayer, 1914; Bayer, 2008; Byosiere, Feng, Chouinard, Howell, & Bennett, 2017; Kasparson et al., 2013; Milgram, 2003; Milgram et al., 1999, 2000; Stevens, 2014; Tapp et al., 2004), and features such as color and

texture are more informative than brightness and size to dogs in form perception (Kasparson et al., 2013; Stevens, 2014). However, the results of the research are often inconsistent. For instance, one study reported that dogs could easily discriminate horizontal and vertical lines but struggled to discriminate upright and inverted triangles (Karn & Munn, 1932). By contrast a recent study found that dogs were able to easily discriminate size differences in a variety of shapes but had problems discriminating horizontal and vertical lines (Byosiere et al., 2017). In such tests, previous experience may affect the salience of different stimuli, so it is difficult to distinguish visual from perceptual limitations. Nonetheless, it is well established that dogs can categorize and differentiate complex visual stimuli, such as human and dog faces (Albuquerque et al., 2016; Autier-Dérian, Deputte, Chalvet-Monfray, Coulon, & Mounier, 2013; Müller, Schmitt, Barber, & Huber, 2015; Nagasawa, Murai, Mogi, & Kikusui, 2011; Range, Aust, Steurer, & Huber, 2008; Somppi et al., 2016) using humanlike cognitive and neural processing (Dilks et al., 2015). The similarities in the neural processing of categorization suggests that once dogs have learned the category specific features, they are likely to generalize in a similar way to humans. However, it is important to be aware that this must be trained in the right way to ensure that the features relevant to humans are the features that the dog is learning.

Conclusion

It is clear that the morphological variation in dogs may significantly influence their visual ability, but this also means there may often be the potential to select for greater ability within the dog gene pool by selecting animals with specific traits for specific tasks. Many apparent limitations in visual perception of dogs compared with humans, such as their perception of certain colors (red/green), or reduced acuity, and increased sensitivity to bright light come with compensations that allow them to outperform humans in other related ways, such as better discrimination of other colors (blue hues), increased motion sensitivity, and superior night vision. Awareness of these differences is essential in both a practical setting to maximize the potential of a human–dog team, in experimental settings to be able to infer that the dogs are using the intended cues to solve a given problem, and in a pet setting to ensure that the owner has appropriate expectations of their animal.

Conflicts of Interest

No conflicts of interest are declared by the authors.

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COMPARATIVE COGNITION & BEHAVIOR REVIEWS

Supplementary Information

Functional Performance of the Visual System in Dogs and Humans: A Comparative Perspective

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SUPPLEMENT 1

Physical Features of Light and Definitions

Light can be characterized by measurements in frequency (Hz), wavelength (nm), and luminous intensity (cd/m^2). Animals are able to see only a small range of wavelengths of full light spectrum, the *visible light*. The spectrum of visible light differs between species, with some animals capable of perceiving and processing wavelength in the region of infrared (700–1000 nm), such as fish (Matsumoto & Kawamura, 2005), snakes (Gracheva et al., 2010), and vampire bats (Gracheva et al., 2011) or ultraviolet light (10–400 nm), such as bees (von Helversen & Edrich, 1974), reindeer (Hogg et al., 2011), and birds (Hunt, Wilkie, Bowmaker,

& Poopalasundaram, 2001), thus exceeding the human spectrum of visible light (400–700 nm; Wolfe et al., 2010). Different wavelengths will be detected by the mammalian visual system as *colors*, as specific retina photoreceptors are tuned to specific wavelength. When transition between two mediums (e.g., air to water) light can be *refracted*. The refractive power/index of a medium is measured in *dioptr*e, which is determined by (a) the structure of the material (e.g., water has a higher refractive index than the air) and (b) the shape of the material (e.g., if a surface of a medium is bent like lenses, light is converged [convex lenses] or diverged [concave lenses]).

SUPPLEMENT 2

Differences in the Anatomy of the Visual System and Pathway of Humans and Dogs and Their Impact on Performance

Ontogeny and Aging of the Eye

The retina develops as a neuroectodermal outgrowth of the prosencephalon (brain), but there are species differences in postpartum maturity. The dog retina matures on average around 56 days postpartum (Evans & De Lahunta, 2013), whereas the human retina matures on average around 105 days postpartum at the earliest (Hendrickson & Yuodelis, 1984). Considering the gestation period (dogs = 63 days on average, humans = 280 days on average) plus average lifespan (dogs = 13 years on average, humans = 79 years on average), it is reasonable to suggest that the human eye is less developed at birth than the dog eye. Nonetheless, the eyelids are open in humans from the 7th month of gestation, whereas in dogs they remain closed for around two weeks postpartum. Furthermore, in dogs the development of photoreceptors is mature by Day 16–35 postpartum, whereas in humans this process takes up to 315 days postpartum (Beaver, 1999; Hendrickson & Yuodelis, 1984). This protracted developmental process may reflect the greater refinement capacity of human vision, and potentially greater association with higher cognitive functions.

In comparison to human eyes, dog eyes appear to age faster; experience human-comparable lens thickening, hardening, and clouding (e.g., because of damage from UV sunlight); and suffer from similar common eye diseases (e.g., cataracts, macula degenerations, and glaucoma) to the extent that they are now often used as a model for such diseases in humans. Additionally, in both dogs and humans, corneal thickness increases, whereas cell density of the cornea decreases with aging (Kafarnik, Fritsche, & Reese, 2007; Montiani-Ferreira et al., 2003), which may cause changes in the refractive index of these structures. However, there are several species differences in aging: (a) Dog lenses age much faster, with a loss of ~1 dioptre (D) within 2 years (Note: Dioptre is a unit for the optical power of a lens, with 1 dioptre = 1 m⁻¹). (Suzuki & Ishikawa, 1974); (b) dog lenses become myopic (resulting in nearsightedness), whereas human lenses become hyperopic (farsighted) during aging (this change may be supported by related changes in both the cornea and ciliary body; Dubbelman & Van der Heijde, 2001; Hernandez et al., 2016; Pokorny, Smith, & Lutze, 1987); and (c) human lenses, but not dog lenses, accumulate a

yellow pigment during aging that could affect human color vision (Kreuzer & Sivak, 1985; Miller & Murphy, 1995; for further reading, see the **Color Vision** section in the main text).

Of interest, supplementation with antioxidants has shown beneficial effects on refractive error in aging dogs (Wang, Hernandez, Moore, Jackson, & Narfström, 2016), and this may be of practical value for prolonging the working life of dogs dependent on visual functioning.

Eye Size

It is not surprising that the human eye is bigger and possibly more consistent in both size and structure (Magrane, 1977; Riordan-Eva, Cunningham, Vaughan, & Asbury, 2011) compared with the dog eye, where there is much morphological variation between breeds (weight ranging from 1.2 to 90 kg and skull length from 7 to 28 cm; McGreevy, Grassi, & Harman, 2004). But the literature on the relationship between these factors and eye structure is inconsistent: Some authors postulate that dog body size and eye globe size is not correlated (Magrane, 1977) and that the eye radius is fixed at 11 mm (22 mm in diameter) largely regardless of body size and breed (Lord, Schneider, & Coppinger, 2016). More recently it has been reported that canine eye size is influenced by breed appearance. The eye radius has been reported to vary between 9.6 and 11.6 mm, with larger eyes in dogs with a longer skull (Gaiddon, Rosolen, Steru, Cook, & Peiffer, 1991; McGreevy et al., 2004). Although a systematic comparison of the eye size of different dog breeds is not available, dogs with long noses (dolichocephalic breeds like whippets or collies) have relatively larger eye globes than dogs with a middle length (mesocephalic dogs such as Labrador retrievers or dalmatians) or short nose (brachycephalic dogs such as boxers; Cottrill, Banks, & Pechman, 1989; Vosough, Masoudifard, Vajhi, Molazem, & Veshkini, 2008). However, it might be that the relationship is more complex and related to cephalic index (skull length relative to width; McGreevy et al., 2004; Roberts, McGreevy, & Valenzuela, 2010), whereas in humans, head size is more generally correlated with eye size (Larsen, 2009). Differences in eye size can potentially affect visual acuity, which

is important for object detection and localization, for example. Specifically, if other features of the eye, such as those involved in focusing light such as the cornea and lens, do not compensate for differences in eye size, differences in visual acuity can be expected between breeds, but this does not appear to have been investigated in any systematic way in dogs. Further, there are sex differences in the eye length of both dogs and humans. In humans, when compared with male eyes, female eyes are slightly shorter (0.4–0.8 mm; Midelfart, 1996; Tomlinson & Phillips, 1970) but are compensated by a steeper corneal curvature (Larsen, 2009). In dogs, Cottrill et al. (1989) reported no sex differences in eye size, but other researchers have postulated that female dog eyes are longer than male eyes (26.3 mm vs. 20.7 mm; Schiffer, Rantanen, Leary, & Bryan, 1982; Vosough et al., 2008). This large 6 mm difference in length raises the question of whether such a difference could be compensated for by differences in the refractive power of the cornea or whether there are fundamental differences in visual performance as a result of sex. Male dogs tend to have thicker corneas (Montiani-Ferreira et al., 2003), which could be an adaptation to a shorter eye, but its functional significance remains unknown. It is also worth noting that the sample size used to make these generalizations in many of the studies is small. For instance, Vosough et al. (2008) reported on “twelve (six males and six females) 2-year-old healthy dogs with no evidence

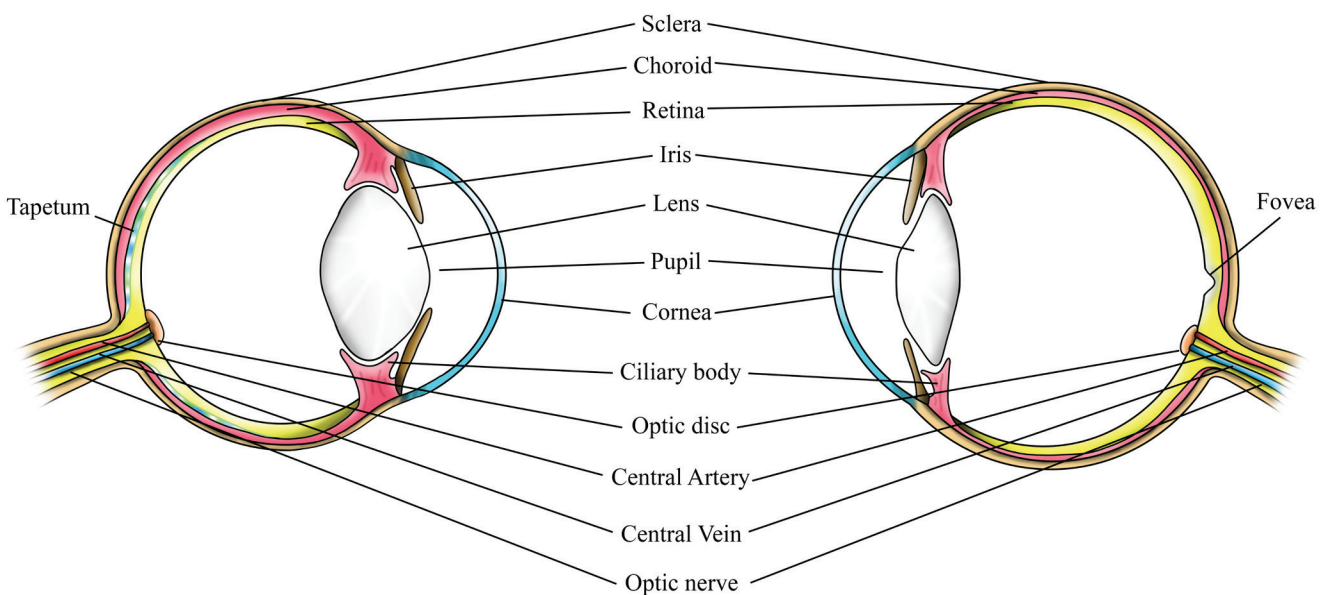
of ocular diseases” (p. 826) and Schiffer et al. (1982) on “17 clinically normal dogs” (p. 92) with no further information on the sample composition (e.g., breeds), which seriously confound the results. For a detailed overview of existing data, see Table S1.

In human females, eye length is further influenced by the oestrous cycle, which has a subsequent impact on visual sensitivity (i.e., changes in corneal thickness and curvature resulting in a change in acuity; Midelfart, 2009), but it remains unknown whether similar changes occur in dogs. This may be of some significance for female working dogs with visually demanding tasks, as they might experience periods of changed visual acuity during the oestrus. Likewise, the effects of neutering do not seem to have been considered.

Cornea

The cornea is the principal refractive structure for converging light within the eye, and even small changes will have significant impact on visual ability. Although the dog cornea is larger and thicker (see Figure S1) than that in humans (Igarashi, 2005), their cell morphology and functioning are similar (Pigatto et al., 2008). The dog cornea is, depending on breed, 12.5–17 mm in diameter (anterior-posterior surface) and 0.6–0.95 mm in central corneal thickness (Magrane, 1977; Tanimura, 1977), indicating extensive variability (see also Table S1).

Figure S1. Schemata of the dog (left) and human (right) eye.



By comparison, the human cornea is much more consistent—on average, 11.5 mm in diameter and 0.55 mm in thickness (Mashige, 2013). The corneal curvature in dogs is also larger (steeper—corneal radius: 8.34 mm–34 mm in dogs [Tanimura, 1977] vs. 6.42 mm in humans [Garner, Owens, Yap, Frith, & Kinnear, 1997]). Consequently, although the cornea refractive index is comparable between dogs (1.375; Coile & O’Keefe, 1988) and humans (1.376; Hecht & Zajac, 1987), the cornea refractive power differs greatly between the two species (41 D in dogs vs. 22 D in humans; Maggs, Miller, Ofri, & Slatter, 2013). It is not known whether the variation in corneal size and shape is compensatory for other morphological changes in the eye that affect acuity (e.g., differences in the focusing capacity of the lens), or simply a potentially pathological artifact because of relaxed selection for visual ability in certain breeds, which would mean that there might be large variation in visual acuity between individuals.

There appear to be sex differences in corneal structure, although these are inconsistently reported in the human literature (Aghaian, Choe, Lin, & Stamper, 2004; Durkin, Tan, Casson, Selva, & Newland, 2007). It has been suggested that male humans have thicker corneas (Garcia-Medina et al., 2011; Hahn, Azen, Ying-Lai, & Varma, 2003; Shimmyo, Ross, Moy, & Mostafavi, 2003), but female humans have steeper corneas to compensate for the shorter axial length of the globe (AlMahmoud, Priest, Munger, & Jackson, 2011; for a review, see Mashige, 2013). As already mentioned, corneal thickness and shape are affected by the oestrous cycle in female humans, which alters corneal transparency and its refractive state (Midelfart, 1996). This results in higher visual sensitivity during ovulatory and postovulatory stages than during menstrual and premenstrual stages (Guttridge, 1994). By contrast, little is known about sex differences in dog cornea and its potential impact, although it has been postulated that male dogs have thicker cornea (Montiani-Ferreira et al., 2003).

Pupil and Iris

The pupillary light reflex and its underlying neural pathway are similar in dogs and humans (Whiting et al., 2013), but as an adaptation to scotopic environments, dogs have larger pupils than humans (Magrane, 1977) to allow more light entry. The typical pupil size of humans is between 3 and 6 mm (Spector, 1990; Wyatt, 1995, 2010), but can be less than 2 mm in miotic eyes

(constricted pupil) and 8 mm in mydriatic eyes (dilated pupil; Spector, 1990; Wolfe, Kluender, & Levi, 2010). By contrast, dog pupil size can reach 9–10 mm in mydriatic eyes (Schmidt, 1968; Whiting et al., 2013). The adaptation of the pupil to light is an involuntary reflex associated with the pretectal area in midbrain, which causes both eyes to react simultaneously to a light stimulus, even if only one eye is exposed to a change in light intensity (consensual light response). Failure of this process can indicate serious pathology in the regulation of the eyes, such as damage to the sympathetic nerve supply that will result in constriction of one pupil and a drooping of the related lower eyelid (Horner’s syndrome). The sympathetic nerve supply courses along the neck close to the carotid, and in dogs, damage may arise from the use of check chains and other blunt trauma to the neck associated with poor handling (Bardorf, 2017; van den Broek, 1987).

Regarding the iris, in humans, lighter irises contract more slowly and show shorter latency and faster redilation speed than darker irises (Bergamin, Schoetzau, Sugimoto, & Zulauf, 1998). This may result in eye color-related capability differences in adapting to different light intensities. Furthermore, lighter irises have fewer color pigments and absorb less light; thus in a very bright environment (e.g., snow, desert) this can result in unfocused and scattered light traveling to the retina, possibly resulting in blurred retinal images of the visual environment and decreased contrast sensitivity (Lam & Baranoski, 2006; Reidenbach, Dollinger, Ott, Janßen, & Brose, 2008). This might explain why humans with light irises often report a higher sensitivity to bright environments. The pupils of dogs with lighter irises have been reported to react faster and for longer (Magrane, 1977), but the opposite appears to be the case in humans (Bergamin et al., 1998). The suggestion of the opposite effect in dogs is surprising, and perhaps worthy of replication, although it is also worth noting that one of the few breeds with naturally occurring blue eyes is the husky, which we would expect to be adapted to snowy and therefore bright environments, and a more reactive pupil may protect it against sudden contrast changes. However, this may also be a random genetic effect that has been conserved in the breed for purely aesthetic rather than functional reasons. A systematic evaluation of light sensitivity in dogs and humans with dark and light irises does not appear to have been undertaken, even though this could impact on their working performance (e.g., snowy landscapes or deserts). Given the lack

Table S1. Summary and Comparison of Existing Data on Eye Globe, Cornea, Lens, and Blood Supply of Dog and Human Eyes.

Topic	Measure	Species	Specifications	N	Data	Publication
Eye globe	Mean axial length	Dog	Various breeds, size and age	124	20.43 ± 1.48 mm	Gaiddon et al. (1991)
		Dog	GSD; guide dogs	53	21.92 ± 0.54 mm	Murphy, Zadnik, & Mannis (1992)
		Dog	NA		21.73 mm	Bayer (1914)
		Dog	Beagle, dachshund	30	18–19 mm	Peichl (1992a)
		Dog	GSD, Doberman	7	22–26 mm	Peichl (1992a)
		Dog	Various breeds, size and age	50	20.9 mm	Nowak & Neumann (1987)
		Dog	Clinically normal dogs	32	21.6 ± 0.77 mm	Schiffer et al. (1982)
		Dog	Labrador retrievers	57	22.12 mm	Mutti et al. (1999)
		Dog	Various breeds, size and age	82	19.12–23.14 mm	McGreevy et al. (2004)
		Human	Vital eyes, males, ages 21–40 years		22.71 ± 1.21 mm	Bhardwaj & Rajeshbhai (2013)
		Human	Vital eyes, females, ages 21–40 years		22.99 ± 0.9 mm	Bhardwaj & Rajeshbhai (2013)
		Human	Various age, postmortem	509	24.44 ± 1.03 mm	Augusteyn et al. (2012)
		Human	NA		23.3 mm	Atchison & Smith (2000)
		Human	NA		24 mm	Deering (2004)
			Mean volumen	Dog	NA	
Human	NA				6 cm ³	Riordan-Eva et al. (2011)
	Weight	Dog	NA		4–8 g	Magrane (1977)
		Human	NA		7–8 g	Riordan-Eva et al. (2011)
Cornea	Corneal thickness	Dog	Various breeds, size and age	59	620 µm	Gwin, Lerner, Warren, & Gum (1977)
		Dog	Various breeds, size and age	37	585 µm	Kafarnik et al. (2007)
		Human	Caucasians (M age = 38 years)	1482	553 µm	Shimmyo et al. (2003)
		Human	Caucasians	36	563 µm	Aghaian et al. (2004)
	Mean corneal radius	Dog	Various breeds, size and age		39.94 ± 2.61 D	Gaiddon et al. (1991)
		Dog	GSD (guide dog)	53	36.67 ± 1.35 D	Murphy et al. (1992)
		Dog	NA		39.71 D	Bayer (1914)
		Human	Caucasians, ages 5–80 years	454	43 D	Fledelius & Stubgaard (2009)
		Human	NA		51.8 D	Hecht & Zajac (1987)
		Dog	GSD (guide dog)	53	9.2 ± 0.67 mm	Murphy et al. (1992)
		Dog	NA		8.5 mm	Bayer (1914)
		Dog	Various breeds, size, and age	50	8.77 mm	Nowak & Neumann (1987)
		Human	NA		7.72 mm	Deering (2004)
		Human	NA		7.06–8.66 mm	Mashige (2013)
Human	NA		7.3 mm	Hecht & Zajac (1987)		

(continues)

Table S1. Summary and Comparison of Existing Data on Eye Globe, Cornea, Lens, and Blood Supply of Dog and Human Eyes.

Topic	Measure	Species	Specifications	N	Data	Publication
Cornea (continued)	<i>Astigmatism</i>	Dog	Various breeds, size, and age	124	Mild, symmetric astigmatism in majority of dogs	Gaiddon et al. (1991)
		Dog	NA		All dogs are astigmatic	Magrane (1977)
		Human	< 95% Caucasians, male and female, ages 5–90 years	3,841	Mild astigmatism (≥ 0.25 D) in about 92% of human	Sanfilippo et al. (2015)
Lens	<i>Axial length</i>	Dog	Labrador retrievers	57	7.83 mm	Mutti et al. (1999)
		Dog	NA	6	7.83 ± 0.45 mm	Kreuzer & Sivak (1985)
		Dog	Clinically normal dogs	32	7.14 ± 0.3 mm	Schiffer et al. (1982)
		Human	NA		4 mm	Hecht & Zajac (1987)
		Human	NA		3.5 mm	Atchison & Smith (2000)
	<i>Anterior curvature</i>	Dog	NA	6	7.29 ± 0.89 mm	Kreuzer & Sivak (1985)
		Dog	Labrador retrievers	57	7.65 mm	Mutti et al. (1999)
		Human	NA		11 mm	Atchison & Smith (2000)
		Human	NA		8.7 mm	Hecht & Zajac (1987)
	<i>Posterior curvature</i>	Dog	NA	6	-6.72 ± 0.75 mm	Kreuzer & Sivak (1985)
		Dog	Labrador retrievers	57	-8.2 mm	Mutti et al. (1999)
		Human	NA		-6 mm	Atchison & Smith (2000)
		Human	NA		-6.3 mm	Hecht & Zajac (1987)
Blood supply	<i>Main retinal artery and veins</i>	Dog			4–5 lateral arteries and 1 central vein	May (2008)
		Human			1 central artery and 1 central vein	May (2008)

Note. GSD = German shepherd dog; D = diopters; NA = not applicable.

of scientific evaluation, it is advisable to protect dog eyes with tinted lenses in bright environments regardless of their eye color, if not to improve performance then to protect the eyes from longer term damage.

In the extreme pigmental circumstance of albinism, individuals often have impaired vision and are especially sensitive to light or even photophobic (Rubin, 1989). A special form of albinism in dogs is the merle-factor, a coat color becoming increasingly popular in several breeds, including collies, in recent years. If an individual is homozygous for this gene, severe ocular health issues can arise (e.g., hypoplasia, coloboma, microphthalmia or

even blindness; Rubin, 1989); in heterozygotes, the extent to which the merle gene affects visual performance in dogs remains largely unknown. However, as a precaution, it may be worth avoiding this eye type if possible.

Another feature unique to dogs is the arterial ring surrounding the canine iris, which contains nerve fibers and supplies oxygen and nutrition to the ciliary body (Evans & De Lahunta, 2013; Magrane, 1977). The blood vessels and nerve fibers in this area might scatter or absorb light with opposing consequences for visual performance, and to date there appears to have been no evaluation of this.

Lens and Ciliary Body

The lens is a dynamic structure responsible for flexibly focusing light at different distances. This structure differs greatly between dogs and humans (see also Figure S1). The ratio of lens-to-globe is 1:18 in dogs but 1:10 in humans (Beaver, 2009), the lens diameter is 9.5–11 mm (breed dependent) in dogs but 11 mm in humans (Magrane, 1977), its anterior-posterior length (thickness) is ~7 mm in dogs but ~4 mm in humans (Coile, 2007; Igarashi, 2005; Mutti et al., 1999), and its anterior radius of curvature is 7.6 mm in dogs (Mutti, Zadnik, & Murphy, 1999) but 12 mm in middle-aged humans (Brown, 1974; Dubbelman & Van der Heijde, 2001; see also Table S1). Furthermore, in comparison with humans, the composite fibers of the dog lens are arranged to have a less flexible structure (Magrane, 1977; Miller & Murphy, 1995), and the ciliary body that controls the dynamic shape of the lens is also weaker (Magrane, 1977). This leads to poorer visual accommodation ability in dogs (2–3 D; dioptre measures the distance at which an object is brought into focus, 3 D accounts for a focus at $\frac{1}{3}$ m) than in humans (14 D in children; Adler & Hart, 1992; Cook, 2009; Dukes & Reece, 2004; Miller, 2001). Thus, dogs can be expected to be less able to focus on objects moving toward them rapidly.

Surprisingly, the dog lens is UV-transmissive (i.e., UV wavelength around 335 nm can still pass to the retina; Douglas & Jeffery, 2014). There is no direct experimental evidence to demonstrate dogs have specific UV-tuned photoreceptors but given that the mammals short-wavelength photoreceptors (responsible for the perception of the blue/violet hue; see also Jacobs, Deegan, Crognale, & Fenwick, 1993) are sensitive to parts of the UV spectrum plus the fact of a UV-transparent lens in dog eyes, it can be assumed that UV light appears to dogs as a blue/violet hue. The human lens is not permeable to UV, and this feature is associated with higher visual acuity from the retina (Douglas & Jeffery, 2014). The function of UV permeability in animals without UV receptors has not been well evaluated. Nevertheless, it is plausible that dogs might perceive UV to a degree at the extreme photoreceptor range. This might be functionally valuable, allowing dogs to see features in the environment that are invisible to humans (e.g., fluorescent traces of DNA or drugs) even if the visual features are poorly resolved. Given the significance of this, it is suggested that attention should be given to the ability of dogs to perceive the UV spectrum.

Retina

The retina is the light sensitive cell layer in the eye responsible for the initial processing and filtering of visual information before it is transferred to the brain. In adult humans the retina is 1094 mm² and has a relatively even dimension of 22 mm from anterior to posterior pole, covering 72% of the eye globe (see also Table S2; Kolb, 1995). This results in good visual field coverage, above, below, and to the sides. The human retina is supplied by one central artery and vein, which arise through the blind spot, a region without photoreceptors that serves as the exit point for optic nerve axons (May, 2008). In dogs the retina is much smaller, ranging from 430 to 837 mm² but with a greater maximum dimension of 25–34 mm depending on breed, which results in good lateral vision but more limited vision in the vertical plain. The dog retina typically has four to five lateral arteries with one central vein (May, 2008) and a more varied blood vessel pattern than in humans, converging toward the central area from all sides (as in humans; May, 2008) or approaching a horizontal line from above and below, and with limited radial convergence toward the central area (Peichl, 1992b).

A detailed summary of existing studies and data on the retina is provided in Table S2.

Retina Cell Composition: Photoreceptors and Ganglion Cells

The retina consists of two types of photoreceptors: cones, which facilitate daytime (photopic) vision, and rods, which underpin low-light (scotopic) vision. The human retina consists of ~5 million cones and 92 million rods (Curcio, Sloan, Kalina, & Hendrickson, 1990), with the highest density of cones in the fovea, a rod-free area with the highest visual acuity in good light conditions but a blind spot in night vision. Photoreceptor density of both rods and cones decreases toward the periphery of the fovea (Curcio et al., 1990). The area around the fovea (macula lutea, yellow spot) is characterized by yellow pigments (lutein and carotenoids), which filter shorter wavelengths and subsequently improve visual acuity by reducing chromatic aberration and prevent possible harmful UV irradiation (Bowmaker, 2002; Kolb, 2018). Humans have trichromatic vision (three types of cone receptors): L-cones (red) reacting to ~560 nm peak wavelength, M-cones (green) to ~530 nm, and S-cones (blue) to ~420 nm (Bowmaker & Dartnall, 1980; Kolb, 2018).

Table S2. Summary and Comparison of Existing Data on the Retina of Dog and Human Eyes.

Topic	Measure	Species	Specifications	N	Data	Publication	
Retina	<i>Retinal area</i>	Dog	Various breeds, size, and age	82	461–683 mm ² (<i>M</i> = 599 ± 49)	McGreevy et al. (2004)	
		Dog	Beagle	1	430 mm ²	Peichl (1992a)	
		Dog	GSD	1	790 mm ²	Peichl (1992a)	
		Dog	Beagle	9	706–837 mm ² (<i>M</i> = 746 mm ²)	Mowat et al. (2008)	
		Wolf	Various subspecies	2	740 mm ²	Peichl (1992a)	
		Human	NA		1,094 mm ²	Kolb (1995)	
		Human	NA	46	1,204 ± 184 mm ²	Panda-Jonas et al. (1994)	
		Human	Postmortem, ages < 37 years	6	1,011 ± 68 mm ²	Curcio & Allen (1990)	
	<i>Total number of ganglion cells</i>	Dog	Various breeds, size, and age	82	48,879–94,033 cells (<i>M</i> = 75,157 ± 12,505 cells)	McGreevy et al. (2004)	
		Dog	Beagle	1	121,000 cells	Peichl (1992b)	
		Dog	GSD	1	110,000 cells	Peichl (1992b)	
		Dog	NA		148,303 cells	May (2008)	
		Wolf	Various subspecies	2	199,000 cells	Peichl (1992b)	
		Human	NA		70,000–1,500,000 cells	May (2008)	
		Human	Postmortem, ages < 37 years	6	1,070,000 ± 400 cells	Curcio & Allen (1990)	
		<i>Mean ganglion cell density</i>	Dog	Beagle	1	280 cells/mm ²	Peichl (1992b)
	Dog		GSD	1	140 cells/mm ²	Peichl (1992b)	
	Wolf		Various subspecies	2	270 cells/mm ²	Peichl (1992b)	
	Human		Postmortem, ages < 37 years	6	1,060 ± 400 cells/mm ²	Curcio & Allen (1990)	
	<i>Streak vs. area centralis</i>	Dog	Beagle, GSD			Moderate or pronounced depending on breed line	Peichl (1992b)
		Dog	Dachshund, boxer, basset, dobermann, Entlebucher			Moderate streak	Peichl (1992b)
		Wolf	Various subspecies			Pronounced streak	Peichl (1992b)
		Dog	Various breeds, size, and age			Retinal topography dependent on cephalic index and skull length	McGreevy et al. (2004)
	<i>Ganglion cell density in area centralis/fovea</i>	Dog	Various breeds, size, and age	82	Weak to strong area centralis: 880–2,640 cells/mm ² ; <i>M</i> = 1,466 ± 440 cells/mm ²)	McGreevy et al. (2004)	
		Dog	Beagle	5	9,100–14,400 cells/mm ² (<i>M</i> = 11,120 cells/mm ²)	Peichl (1992b)	
		Dog	GSD	3	7,500–14,300 cells/mm ² (<i>M</i> = 11,500 cells/mm ²)	Peichl (1992b)	
		Dog	Dachshund, Entlebucher	2	6,400, 8,600 cells/mm ²	Peichl (1992b)	
		Dog	GSD	12	5,300–13,000 cell/mm ²	Gonzalez-Soriano et al. (1995)	
Wolf		Various subspecies	2	13,000 cells/mm ²	Peichl (1992b)		
Human		Postmortem, ages < 37 years	6	31,600–37,800 cells/mm ² (<i>M</i> = 35,100 cells/mm ²)	Curcio & Allen (1990)		

Topic	Measure	Species	Specifications	N	Data	Publication	
Retina <i>(continued)</i>	<i>Ganglion cell density in periphery per mm²</i>	Dog	Various breeds, size, and age	82	484 ± 163 cells/mm ²	McGreevy et al. (2004)	
		Dog	Various breeds, size, and age	82	Weak to strong area centralis: 880–160 cells/mm ²	McGreevy et al. (2004)	
		Dog	Various breeds, size, and age	1	Weak to strong area centralis: ~2,000–500 cells/mm ²	Peichl (1992b)	
		Dog	GSD	12	≤ 500 cell/mm ²	Gonzales-Soriano, Rodriguez-Veiga, Martinez-Sainz, Mayayo-Vicente, & Marin-Garcia, et al. (1995)	
		Human	Postmortem, ages < 37 years	6	Development of streak possible and varies individually	Curcio & Allen (1990)	
		<i>Alpha-cell density central area per mm²</i>	Dog	NA		170 cells/mm ²	Peichl (1991)
		<i>Alpha-cell density peripheral area per mm²</i>	Dog	NA		< 5 cells/mm ²	Peichl (1991)
	Rods and cones	<i>Total number of cones</i>	Human	NA		5,000,000	Deering (2004)
			Human	Postmortem, ages 27–44 years	7	4,080,000–5,290,000	Curcio et al. (1990)
			Human	Normal donor eyes	46	3,246,000 ± 618,000	Panda-Jonas et al. (1994)
Dog			NA		NA	NA	
<i>Total number of rods</i>		Human	NA		80,000,000	Deering (2004)	
		Human	Postmortem, ages 27–44 years	7	78,000,000–107,000,000	Curcio et al. (1990)	
		Human	Normal donor eyes	46	57,447,000 ± 10,481,000	Panda-Jonas et al. (1994)	
		Dog	NA		NA	NA	
<i>Cone density area centralis</i>		Dog	Beagle		9	23,080 ± 1,593 cells/mm ²	Mowat et al. (2008)
		Human	Postmortem, ages 27–44 years		7	199,000 cells/mm ² (100,000–324,000 cells/mm ²)	Curcio et al. (1990)
		Human	Postmortem, ages < 37 years		6	205,000 cells/mm ²	Curcio & Allen (1990)
<i>Cone density periphery</i>		Dog	Beagle		9	7,465 ± 726 cells/mm ²	Mowat et al. (2008)
		Human	Postmortem, ages 27–44 years		7	5,000 cells/mm ²	Curcio et al. (1990)
<i>Rod density in area centralis</i>		Dog	Beagle		9	501,000 ± 20,180 cells/mm ²	Mowat et al. (2008)
		Human	Postmortem, ages 27–44 years		7	None — rod-free area	Curcio et al. (1990)
<i>Rod density in periphery</i>		Dog	Beagle		9	304,800 ± 28,700 cells/mm ²	Mowat et al. (2008)
		Human	Postmortem, ages 27–s44 years		7	15–20,000 cells/mm ²	Curcio et al. (1990)
<i>M/L/S ratio in general</i>		Human	NA			0.3:0.62:0.08	Deering (2004)
	Human	NA			2.88:1:0.17	Roorda, Metha, Lennie, & Williams (2001)	

(continues)

Table S2. Summary and Comparison of Existing Data on the Retina of Dog and Human Eyes. (*Continued*)

Topic	Measure	Species	Specifications	N	Data	Publication
Rods and cones (<i>continued</i>)	M/L/S ratio in general (<i>continued</i>)	Dog	Various breeds, size, and age	82	15-20:1	McGreevy et al. (2004)
	<i>ML/S ratio in area centralis</i>	Dog	Beagle	9	4.5:1	Mowat et al. (2008)
	<i>ML/S ratio in periphery</i>	Dog	Beagle	9	9.1:1	Mowat et al. (2008)
	<i>Rod/cone ratio area centralis</i>	Dog	Beagle	9	23:1	Mowat et al. (2008)
		Human	Postmortem, ages 27–44 years	7	Rod free	Curcio et al. (1990)
	<i>Rod/cone ratio periphery</i>	Dog	Beagle	9	41:1	Mowat et al. (2008)
		Human	Postmortem, ages 27–44 years	7	30:1	Curcio et al. (1990)
	<i>Cone:ganglion cell ratio area centralis/fovea</i>	Human	Postmortem, ages < 37 years	6	2.6:1	Curcio & Allen (1990)
		Dog	NA		NA	NA
	<i>Cone:ganglion cell ratio in periphery</i>	Human	NA		16:1	Miller & Murphy (1995)
Dog		NA		NA	NA	

Note. GSD = German shepherd dog; NA = not applicable.

S-cones are not found in the central fovea, preventing chromatic abbreviation and enabling higher visual acuity (Calkins, 2001). Rods provide visual information in lower light conditions and have peak sensitivity to ~496 nm wavelength (Kolb, 2018; Van Buren, 1964).

By contrast, dogs have rods distributed throughout the entire retina (Coile, 2007; Cook, 2009; Miller, 2001; Miller & Murphy, 1995; Neuhaus & Regenfuss, 1967; Yamaue, Hosaka, & Uehara, 2015). Although they do have an area centralis, a region with the highest density of cones, it does contain some rods and consequently daytime visual acuity is reduced, but so too is the risk of a blind spot in nighttime vision. Depending on the breed, the centralis can range from a relatively round humanlike area to a more nasally and temporally distributed region to create a streak-like area of maximal visual acuity for the individual (see **Topographical Mapping of the Retina** section). There is no yellow spot in the dog retina (Beaver, 2009; Jacobs et al., 1993), which could have implications for visual acuity as short wavelengths are not filtered and may be scattered, possibly causing a blurred retinal image. Behind

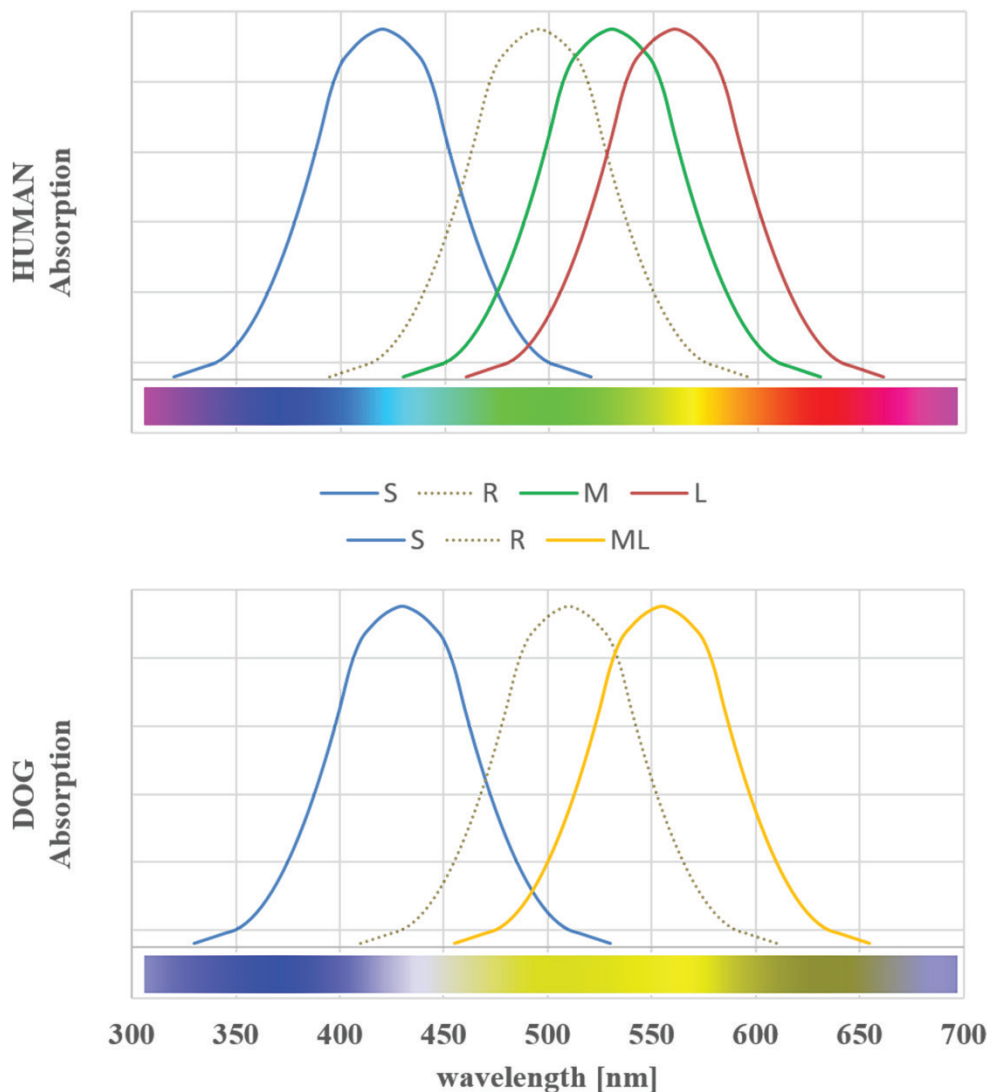
most of the photoreceptors in dog eyes there is a tapetum lucidum, a light reflective cell layer in the fundus of the eye that increases the use of light energy within the retinal area and so enhances scotopic vision but at the expense of visual acuity because of increased light scatter during photopic vision (Yamaue et al., 2015). Rods in dog retina react strongest to a slightly different wavelength to humans (510 nm vs. 496 nm, see Figure S2; Coli & Marroni, 1996; Kemp & Jacobson, 1992; Miller & Murphy, 1995). However, as this difference is only 15 nm between dogs and humans, some authors argue that the enhanced night vision abilities in dogs are due to other visual adaptations (Miller & Murphy, 1995). On the other hand, this difference may lead to different night vision sensitivity; that is, items reflecting at longer wavelengths (e.g., yellow during photopic vision) might be more perceptible to dogs compared with humans. To corroborate this assumption, more research is needed. In general, dogs have a number of adaptations potentially allowing better vision than humans in low-light conditions (e.g., bigger lenses or a tapetum lucidum). Dogs have dichromatic vision (Neitz, Geist, & Jacobs,

1989; Siniscalchi, d’Ingeo, Fornelli, & Quaranta, 2017) with two classes of cone pigments: one reacting to long/medium wavelength (ML-cone, green-yellow hue) with a peak sensitivity at ~555 nm and a second cone reacting strongest to short wavelength at ~429 nm (S-cone, blue-violet hue), meaning they have poor resolution of the color humans see as red (see Figure S2). Of interest, dog S-cones contain additional cryptochromes, which could be important for the circadian clock but also involved in magnetic field sensing (Nießner et al., 2016).

The photoreceptors relay their electrical activities to ganglion cells, which collect, summarize, and transfer those signals via the optic nerve to the visual

cortex. The morphology of the ganglion cell population in the dog retina is similar to the human retina, but it is unclear whether its function is identical (Peichl, 1991, 1992a; Peichl, Ott, & Boycott, 1987). Although there are disagreements about their number (ranging more than threefold from 15,000 to 49,000 cells/mm²; see also Table S2; May, 2008; McGreevy et al., 2004; Peichl, 1992b), it is generally agreed that dogs have fewer ganglion cells and that they serve larger visual fields (i.e., number of summarized photoreceptors) than humans, consistent with the lower visual acuity in dogs. Further, it has been postulated that wolves have up to twice as many ganglion cells as dogs (and therefore possibly

Figure S2. Schematic absorption spectra of photoreceptors and visible color hues in dogs and humans. S = short wavelength cones; M = medium wavelength cones; ML = medium/long wavelength cones; L = long wavelength cones; R = rods.



higher visual acuity) with up to 18% alpha ganglion cells¹ compared with 3%–14% in dogs (and therefore possibly better scotopic vision because of summarization over a large receptive field). This difference might be a consequence of domestication (Peichl, 1992a), but the impact of breed diversity needs to be considered and may explain the variation in the number of cells reported in dogs. Current data are based on anatomical studies with small sample sizes and a limited range of dog breeds, and so the reliability of estimates is questionable.

Topographical Mapping of the Retina

In the human retina, the density of cones decreases from ~200,000 cells/mm² in the fovea to ~5,000 cells/mm² toward the periphery (Curcio et al., 1990). There are more cones nasally than temporally, and a relative streak of high cone density can be found along the horizontal meridian (Curcio & Allen, 1990). The highest rod density is also found surrounding the horizontal meridian as well as nasally to the optic disc and fovea (176,000 cells/mm²) with a decline towards the periphery (~17,000 cells/mm²; Curcio et al., 1990). The density distribution of ganglion cells mirrors that of photoreceptors, with the highest density in the central retinal area around the fovea and optic disc (35,000 cells/mm²). Density is 300 times higher in the nasal than the temporal area, declining toward the periphery (250 cells/mm²).

In the dog retina, the position and extent of the area centralis is highly dependent on breed morphology: Brachycephalic dogs and dogs with low cephalic indices have a pronounced area centralis, whereas dolichocephalic dogs and dogs with high cephalic indices have a less pronounced area centralis and more of a horizontal streak (visual streak; McGreevy et al., 2004). However, dogs of the same breed or even from the same litter can develop either a visual streak or area centralis, and it is unclear why this individual difference may occur (Peichl, 1992b; Willis et al., 2001), although the potential for functional adaptation based on experience needs to be considered, which may have implications for the management of dogs used in tasks associated with different visual abilities. The ML-cones density in the area centralis is ~23,000 cells/mm² (~10 times lower than

in human fovea) and ~6,500 cells/mm² in the periphery (data only from beagles; Mowat et al., 2008) and is higher in the temporal than nasal area (especially in brachycephalic breeds; McGreevy et al., 2004). Of interest, the ML-cones are denser in the area centralis and the surrounding temporal areas in brachycephalic breeds but are more concentrated in the nasal area in dolichocephalic breeds (McGreevy et al., 2004). Such a distribution difference could influence visual acuity and color vision between these dog breeds (see the **Visual Acuity and the Color Vision** section in the main text). S-cone density is ~2,000 cells/mm² throughout the retina (Mowat et al., 2008) but unlike ML-cones without higher densities in the temporal area (McGreevy et al., 2004). The peak density for rods is ~500,000 cells/mm² in the central area and ~31,000 cells/mm² in the periphery (more than 2 times higher than in human fovea and periphery; data on beagles; Mowat et al., 2008). These high concentrations of rods and S-cones but low concentrations of ML-cones come at the cost of lower visual acuity compared with humans during photopic vision. This lower visual acuity has been determined in behavioral but also neurobiological studies (also see the main text).

Another unique feature of the dog retina is an alpha ganglion cell gap in the temporal retina. Unlike other mammals, dogs do not have alpha ganglion cells in this retinal region, but other types of ganglion cells are found. Related functional deficits in visual acuity, movement detection, and depth perception have been assumed but not investigated (Miller & Murphy, 1995; Peichl, 1991, 1992b). It is also assumed that the visual streak is an archetypical feature that allows dogs to see sharply along the horizon for hunting (Ahnelt & Kolb, 2000; Lind, Milton, Andersson, Jensen, & Roth, 2017; Miller, 2001; Peichl, 1992b), whereas an area centralis allows sharp vision in a small circular proportion of the visual field, which may be advantageous for close visual analysis of structures like faces. The latter is more common in brachycephalic breeds, who also have more frontally placed eyes, and many of these breeds are typically “lap dogs,” for whom attending to human faces could be advantageous. However, this may also come at a cost: during development, ganglion cells and cones are produced early and evenly distributed within the eye; only later are rods added over a relatively short time to the central retinal area (although over a longer period to the peripheral retina). For the development of the area centralis, this may mean that individuals have lower densities of rods (McGreevy et al., 2004) with functional consequences on their scotopic visual performance.

² Alpha ganglion cells have been assumed to be specialized evolutionary correlates of primates Y (in humans M cells), which are characterized by large dendritic and therefore large receptive fields. For further reading, see Boycott and Wässle (1974); H. Kolb (2018); B. B. Lee, Martin, and Grünert (2010); and Leventhal, Rodieck, and Dreher (1981).

Tapetum Lucidum

The tapetum lucidum, which reflects light back into the eye from the back of the retina, is a common feature of animals adapted to see in low-light conditions and is found in dogs (e.g., see Figure S3) but not in humans. It is an iridescent cellular layer, situated slightly dorsally to the optic disc (Hebel, 1976). It provides the retinal photoreceptors with an additional opportunity to be stimulated by photons that have already passed the receptors and therefore increases retinal sensitivity in low-light conditions. The dog tapetum is shaped like a rounded triangle and consists of polygonal plates arranged like “bricks in a wall.” It occupies about 30% of the fundus, has up to 20 cell layers in the center (thinner toward the periphery), and is overlaid by the highest densities of rods (Lesiuk & Braekevelt, 1983; Ollivier et al., 2004; Yamaue et al., 2015). Smaller dog breeds have proportionally smaller tapetal areas (Granar, Nilsson, & Hamberg-Nyström, 2011). The tapetum color varies from yellow-green to blues and orange (Granar et al., 2011).

Dogs and cats tapetum have been described as similar (even though they diverge in size; dog tapetum coverage = ~30%, cats = ~50%; Ollivier et al., 2004). Consequently, it has been argued that the dog tapetum has a similar 44% reflective ability as the cat tapetum (Schmidt, 1968). However, others claim that the dog tapetum is less effective than the cat because of an uneven arrangement of the cellular “bricks” (Lesiuk & Braekevelt, 1983). The reflecting properties of the tapetum cellulose are based on interference at the regularly spaced intracellular rodlets. The dog tapetum is a spectral filter because of the spacing of these elements, as evidenced by the tapetal colouration. However, measurements and calculations for the structurally similar tapetum of the cat suggest that the tapetal influence on retinal spectral sensitivity is marginal (Gunter, Harding, & Stiles, 1951; Weale, 1953), but other views also exist (Coles, 1971). There are also possible differences in composition of dogs’ and cats’ tapetum accounting for functional differences (for a review, see Ollivier et al., 2004). Cats’ tapetum contains riboflavin, which enables wavelength shifts via fluorescence to rod sensitivity maximum; that is, tapetal riboflavin absorbs shorter wavelengths (blue, ~450 nm) and shifts it via fluorescence to a longer wavelength (~520 nm), which is closer to the rod sensitivity maximum (Miller and Murphy, 1995; Ollivier et al., 2004; Schmidt, 1968). This can be imagined as an additional amplification of the available light next to its twofold use. Dogs’ tapetum contain zinc cysteine, but riboflavin has not been reported, making it uncertain

if wavelength shifts occur in dogs’ eyes and if their low-light abilities are similar to cats. However, final clarification is needed to clarify if riboflavin is a general feature of all carnivore eyes.

Further, in a population of 539 Swedish dogs of various breeds and ages, it was shown that only 70.9% of the dogs had a full tapetal area, and in ~2% of the dogs the tapetum was missing completely (Granar et al., 2011). The appearance of a tapetal area is thereby not dependent on breed and might show local differences (e.g., in thickness and strength of pigmentation) within the eye of an individual. Dogs without a tapetum have not been reported to have impaired vision in dim-light conditions, but the relevance of these findings to working dogs requiring high visual acuity in different environments should be considered (Miller & Murphy, 1995).

Besides the advantages of the tapetum during low-light conditions, it has been argued that there are also disadvantages of the tapetum, as it may impair vision in bright light conditions due to a scattering of incoming light (Cook, 2009; Hebel, 1976; Miller & Murphy, 1995; Ollivier et al., 2004). However, recent studies have argued that the dog tapetum does not functionally impair peak visual performance in photopic conditions because (a) the visual streak is not located on the thickest part of the tapetum and (b) the reflected wavelengths are not near the absorption maximum of the cones (Yamaue et al., 2015). It must be acknowledged that these results are based on the anatomical observation of only three eyes.

Figure S3. Picture of a dog's eye with reflective tapetum.



Furthermore, the existence of the tapetum, plus the fact that the retinal area behind the tapetum is unpigmented but becomes pigmented toward the periphery, induces local differences in pigmentation, with darker pigmentation in the inferior area (for a review, see Miller & Murphy, 1995). As the superior area perceives light from the usually darker ground and the inferior area from the usually brighter sky, the darker pigmentation in the inferior area might reduce light scattering, whereas the superior area enhances the view of the darker ground (Lesiuk & Braekveelt, 1983). However, it is unknown whether these differences in pigmentation would be problematic when the ground is brighter than normal (e.g., in snow or sand) and whether specialized mechanisms like bridging amacrine cells (Wässle & Boycott, 1991) between the superior and inferior retina could help to equilibrate such differences and distortions. If not, special lenses may be required to accommodate this.

Visual Pathway

Optic Nerve

The axons of the ganglion cells leave the eye at the optic disc and continue their pathway to the brain as the optic nerve fibers. In humans, each optic nerve is composed of up to 1.2 million nerve fibers, and nerve fiber counts are independent of sex or side of the eye but are influenced by age, with a decreasing number of nerve fibers in aged eyes (Bruesch & Arey, 1942; Jonas, Schmidt, Mueller-Bergh, Schloetzer-Schrehardt, & Naumann, 1992). It has been postulated that more nerve fibers would lead to a larger optic disc, which would have implications on visual functioning (Jonas et al., 1992). In dogs, each optic nerve is composed of far fewer (~155,000) nerve fibers compared to humans (Brooks et al., 1995; Bruesch & Arey, 1942), indicating a greater degree of visual information summation from the visual field, consistent with reduced visual acuity but possibly enhanced sensitivity. To our knowledge, there are no investigations regarding sex, eye side, or age differences concerning the number of nerve fibers in dogs, but those with larger eyes may have significantly more nerve fibers (Arey, Bruesch, & Castanares, 1942).

Optic nerve fibers are generally not myelinated within the eye to ensure transparency to photons, which must pass through them to reach the photoreceptors. They are myelinated when leaving the eye at the retino-optic nerve junction, resulting in an enlarged optic disc and blind spot. The mechanism for suppressing myelin growth in the nerve fibers is different in dogs compared

with other animals (Miyake, Imagawa, & Uehara, 2004). In humans, centrifugal and centripetal axons are responsible for bottom-up and top-down responses, respectively (Evans & De Lahunta, 2013), but in dogs the existence of such axons needs confirmation.

Optic Chiasm and Lateral Geniculate Nucleus

The optic nerve passes through the optic chiasm, at the base of the brain where some optic nerve fibers may cross (decussation). The temporal nerve fibers from one eye are combined with the nasal nerve fibers from the contralateral eye so that visual information from a single lateralized field of view is integrated. This not only allows focal localization of related information within the brain but also enables depth perception through the provision of slightly different retinal images from each of the two eyes. The amount of decussation, which is also functionally related to sudden movement detection, depends on the placement of the eyes. Animals with frontally placed eyes have a decussation of 50%–65% (in most predators, at least 50% the brain is presented with two versions of every image), whereas animals with laterally placed eyes have decussation of more than 65% (most prey species; Herron, Martin, & Joyce, 1978). Studies have indicated that humans and dogs have, on average, decussation rates of 50% and 75%, respectively (De Lahunta & Cummings, 1967; De Lahunta, Glass, & Kent, 2014; Evans & De Lahunta, 2013; Herron et al., 1978), but the extent to which decussation reflects variation in eye placement between different dog breeds is largely unknown. Inconsistent with the reported 75% decussation rate, some studies have observed that dog optic nerve fibers project equally to the contralateral and ipsilateral side of the lateral geniculate nucleus (LGN; Kimotsuki, Yasuda, Tamahara, Matsuki, & Ono, 2005), indicating a 50% decussation rate. Further research is needed to clarify the decussation rate at the optic chiasm and its relation to skull morphology (e.g., brachycephalic vs. dolichocephalic) and to examine whether the amount of decussation is related to ecological function or developmental experience.

The LGN is the relay center of the optic pathway in which visual information is reorganized and sorted for the first time. For instance, in the LGN, topographical mapping occurs (neighboring retinal information reaches neighboring brain areas), retinal outputs are distributed according to the size of ganglion cells, and information from rods and cones is separated and reorganized as a result (Evans & De Lahunta, 2013). In dogs this reorganization also relates specifically to photosensitive

cells associated with the tapetum lucidum, the outputs of which are predominantly processed in the medial interlaminar nucleus (Lee, Kim, & Lee, 1999), which is absent in humans (the equivalent region in primates is the interlaminar zone of the LGN; Irvin, Norton, Sesma, & Casagrande, 1986). This organization of the LGN emphasizes that although the principal structure is similar between dogs and humans, there are specializations that may relate to differing functionality between and within breeds (e.g., due to differences in topographical mapping or appearance of tapetum lucidum).

Visual Cortex

The layering and functioning of visual cortex is comparable between dogs and humans: The primary visual cortex provides topographical mapping and cortical magnification of the fovea in humans, and the area centralis and/or visual streak in dogs (i.e., the center of the visual field occupies a larger cortical area; Ofri, Dawson, & Samuelson, 1994). However, given differences in retinal topography and LGN specializations, it is not surprising that there are differences in the visual cortex of dogs and humans. For example, in dogs there

is a distinct cortical region, in the LGN, for processing dim-light vision (Evans & De Lahunta, 2013). However, for both dogs and humans, other information emerging from rods (e.g., movement, size and contrast detection) and cones (e.g., color, visual details) is subsequently processed in specialized cortical regions (the superior and anteroventral cortical region, respectively, in dogs). It should be noted that differences in dog morphology and consequently retinal topography may result in differences in brain mapping (Ofri et al., 1994).

Recent advances in applying functional magnetic resonance imaging (fMRI) on unrestrained, awake dogs (Berns, Brooks, & Spivak, 2012, 2013; Berns, Brooks, Spivak, & Levy, 2016) have promoted investigation of cortical functioning in dogs. To date, a few studies have examined the cortical processing of faces (Dilks et al., 2015) and other emotionally relevant information (Berns et al., 2013; Cook, Prichard, Spivak, & Berns, 2016; Cook, Spivak, & Berns, 2014, 2016). With advances in such techniques and others, such as eye tracking, we will soon be able to comparatively investigate the link between visual processing and cognitive performance for dogs and humans.

SUPPLEMENT 3 Functional Performance of the Visual System

Visual Acuity

Table S3. Overview of Existing Data on Visual Acuity in Dogs and Humans.

Author	Method	Light Regime (cd/m ³)	Species			
			Dog		Human	
			N	Data (Cycles per Degree)	N	Data (Cycles per Degree)
Schmidt (1968)	Moving object	NA	NA	4		
Schmidt (1968)	Stationary objects	NA	NA	2.95		
Neuhaus & Regenfuss (1967)	2-choice discrimination	83	Poodle-mix, N = 1	4.0		
Neuhaus & Regenfuss (1967)	2-choice discrimination	0.23	Poodle-mix, N = 1	6.2		
Odom, Bromberg, & Dawson (1983)	Visually Evoked Cortical Potentials	86	1 mix, 3 beagles	12.6		
Odom et al. (1983)	Pattern-Evoked Retinal Potentials	86	1 mix, 3 beagles	11.6		

(continues)

Table S3. Overview of Existing Data on Visual Acuity in Dogs and Humans. (Continued)

Author	Method	Light Regime (cd/m ³)	Species			
			Dog		Human	
			N	Data (Cycles per Degree)	N	Data (Cycles per Degree)
Ofri, Dawson, & Gelatt (1993)	Pattern-Evoked Retinal Potentials	86	4 beagles	6.9		
Murphy et al. (1992)	Sweep-Visually-Evoked Potential	73	3 beagles	7.1–9.5		
Coile (2007)	NA	NA	NA	4.5–6.0	NA	30–50
Lind et al. (2017)	2-choice discrimination	43	Whippets, N = 4	6.0–17.4	Female Caucasians, N = 4	32.1–44.2
			Pug, N = 1	19.5	Male Caucasians, N = 3	32.7–43.3
			Shetland sheepdog, N = 1	5.5		
Lind et al. (2017)	2-choice discrimination	0.008	Whippets, N = 4	1.8–3.5	Female Caucasians, N = 4	6.7–9.9
			Pug, N = 1	2.1	Male Caucasians, N = 3	5.9–8.7
			Shetland sheepdog, N = 1	NA		
Graham et al. (2019)	Forced-choice preferential looking at 1 m	NA	Mixed breeds, N = 10	6.5		
Graham et al. (2019)	Forced-choice preferential looking at 3 m	NA	Mixed breeds, N = 10	4.7		

Light Adaptation

Table S4. Maximum Permissible Radiation Including Exposure Duration for Light Sources Including Laser and LED after IEC 60825-1:2001-08.

Exposure duration (s)	Max Permissible Power of Light Source (mW)
0.25	1.0
1.0	0.7
10–30,000	0.39

Note: Adapted from Reidenbach et al. (2008); values advised for humans.

Other Responses to Light

Although this review has focused on visual perception, it is worth considering some of the other more general effects of light on the individual, as not all light is processed in relation to specific visual stimuli. Exposure to light has many influences on humans that need to be considered, such as affecting the sleep–wake cycle and resetting the circadian clock (Bedrosian & Nelson, 2017; Duffy & Czeisler, 2009; Stevens & Zhu, 2015). In dogs, dim-light conditions before sleep time can promote sleep, possibly because of changes in melatonin secretion; after exposure to bright light, dogs show more agitated behavior shortly before rising, and temporarily increase resting behavior possibly because of exhaustion (Fukuzawa & Nakazato, 2015). Such results need to be considered in relation to the effective management of lighting for dogs in both home and kennel settings.

SUPPLEMENT 4

Transmission of the Light From the Eye to the Brain

When light is emitted by or reflected from an object, the corresponding light rays are transmitted to the eye by passing through the *cornea*, the clear “front” window of the eye. The cornea is a clear part emerging from the *sclera* (white part of the eyeball). Although the sclera contains blood vessels, the cornea is free of blood vessels to obtain transparency. The cornea contains transparent sensory nerve endings with protective functions, such as controlling eye closure and tear production. It is remarkable to note that the cornea is able to transmit almost 100% of the visible light, whereas, at least in humans, some of the harmful light (e.g., ultraviolet light) is absorbed by embedded glycoproteins (Meek, 2002). The cornea functions as an optical lens and is more curved than the rest of the eyeball. Through the refractive surface, the cornea is responsible for about two-thirds of the focusing of the light in humans (Meek, 2002). An equal spherical surface of the cornea is crucial for focusing rays of light. If the cornea is not spherical, astigmatism occurs, which causes some light rays to be focused in front of the retina and others behind it, resulting in a distorted and blurred vision.

After passing the cornea, bended light rays are transmitted through the *anterior chamber* to the iris. The anterior chamber is filled with the aqueous humor, a clear, watery fluid that derives from blood and is responsible for supplying oxygen and nutrients as well as removing waste from the cornea and the lens. Following the anterior chamber, the light must pass the *pupil*, a hole in the middle of the *iris*. The iris gives the eye its distinctive color and consists of circular and radial muscles regulating the amount of light entering the eye by constriction and dilation of the pupil through pupillary light reflex; in a dark environment, the pupil is automatically dilated to allow more light to enter, whereas in a bright environment, the pupil is automatically constricted. The pupil can further vary in its shape in different species, such as vertical slit in cats, horizontal rectangular pupil in goats, and round pupil in humans and dogs. However, independent of its shape, the pupil’s function is to focus light rays to pass through to the lens.

The *lens* is a flexible, crystalline biconvex structure and is free from blood vessels and therefore transparent. It is controlled by the *ciliary muscles*, which ensure that the lens can change its shape for the purpose of accommodation. This is an important feature of the

eye, as the refractive index of preceding eye features (i.e., cornea, anterior and posterior chamber) are fixed and therefore cannot bring objects at varying distances to a focus. When the ciliary muscles are relaxed, the lens is relatively flat, and the eye is focused on distant objects. However, when the ciliary muscles contract, the lens is bulging, and the focus can be laid on nearby objects. The ability of accommodation is limited by several factors, such as the ability of the ciliary muscles to bend the lens or the composition of the lens itself. These abilities can change in age (e.g., muscles become weaker and lens more inflexible) and cause presbyopia (“old sight”), a form of farsightedness from the loss of the ability for accommodation (see also age effects and dog human comparison of accommodative abilities).

In the next stage of passage through the eye, focused light rays will travel through the *posterior chamber* to the retina. This chamber is the biggest/longest part of the eye (~80% of the eye in humans; Wolfe et al., 2010) and filled with transparent, colorless, and jelly-like fluid, the vitreous humor, which keeps the eyeball in its shape. The length of the eye chamber in addition to the refractive power of the cornea is critical for emmetropia, the condition of normal sightedness, in which the light rays focus exactly on the retina. If the features of the eye do not match perfectly, the perceived image is blurred. For example, if the eyeball is too long, the image is focused in front of the retina and distant objects cannot be seen sharp (nearsightedness, myopia), whereas if the eyeball is too short, the picture comes into focus behind the retina and near objects cannot be seen sharp (farsightedness, hyperopia). Spectacles with lenses accordingly to the refractive error can compensate for this mismatch.

At the end of the posterior chamber the light is projected onto the *retina*. The retina is composed of a complex layer of photoreceptors (rods and cones), which interconnect via a series of interneurons (bipolar, horizontal, or amacrine cells) to a layer of ganglion cells, which axons form the optic nerve. When the light hits the *photoreceptor layer* of the retina, the energy of the light is transduced into electric neuronal signals. In mammalian eyes there are two important classes of photoreceptors, which are tuned to different wavelengths. The rods, containing the photopigment rhodopsin, are tuned to wavelengths at around 500 nm and are important for scotopic vision and movement detection. A rod can react

to a single photon, but normally the response of several rods is pooled together. In the subsequent processing of the visual stimuli by the ganglion cells, this results in large receptive fields, the area in which visual stimulation will cause a ganglion cell to fire but consequently lead to poor spatial resolution of the visual environment. On the other hand, the cones can be tuned to several wavelengths, depending on the chemical composition of its photopigment cone opsin. They can be sensitive to wavelength covering the full spectrum of the visible light. Cones, compared with rods, require higher levels of illumination and are therefore important for photopic and color vision. Further, cones have small receptive fields and are therefore important for high spatial resolution of the visual environment. For this reason, cones are often found to be present in regions that are important for the visual acuity; for example, in humans they are predominantly found in the *fovea*, a region directly behind the center of the pupil. Most mammalian retinas are dominated by rods, but ratio of rods and cones as well as their distribution depend on whether an animal is primarily tuned to a diurnal or nocturnal live style.

When the light hits a photoreceptor, it is absorbed by the photopigment and a biochemical cascade causes a hyperpolarization of the cell. This subsequently causes a reduction of neurotransmitter at the synaptic gap to the *interneurons*. The most important interneuron is the bipolar cell. There are two types of bipolar cells: diffuse bipolar cells receiving input from several rods and midget bipolar cells receiving input from a single cone. Bipolar cells can be divided into ON or OFF bipolar cells. The ON bipolar cells respond to light, and OFF bipolar cells respond to the absence of light. For this reason, these bipolar cells are important for the detection of changes in illumination, respectively movement detection. Other interneurons are responsible for the connection between the nearby photoreceptors (e.g., horizontal cells are important for lateral inhibition; Wolfe et al., 2010) or between amacrine, bipolar, and ganglion cells (e.g., the precise function of amacrine cells is not clear but is possibly for contrast enhancement and temporal sensitivity; Wolfe et al., 2010).

In the final processing of the light stimulus in the retina, responses of interneurons are transduced to *ganglion cells*. Out of several types of ganglion cells, two are most important: The first type is large cells receiving input from several photoreceptors (large receptive fields, brisk transient reaction upon constant stimulation, long latency) and is therefore important for the detection of illumination changes over time. In humans these

ganglion cells are called M (magnocellular) ganglion cells, whereas in monkey, cats, and canines the analogue cell is called alpha or Y ganglion cells (Boycott & Wässle, 1974; Peichl, 1991; Van Hooser, Heimel, & Nelson, 2003). These large ganglion cells increase in number toward the periphery of the retina. The second type are small cells receiving input only from single photoreceptors (small receptive field, brisk sustained reaction upon constant stimulation, short latency) and is therefore important for the resolution of details. In humans these ganglion cells are called P (parvocellular) ganglion cells, whereas in monkeys, cats, and canines the analogue cell is called beta or X ganglion cells (Boycott & Wässle, 1974; Peichl, 1991; Van Hooser et al., 2003). These small ganglion cells are predominantly found in regions important for visual acuity, such as the fovea. Ganglion cells, as bipolar cells, can be also divided into ON and OFF cells, whereas the difference is that the ON- and OFF-center react to several photoreceptors compared with a single photoreceptor as in bipolar cells. This organization of cells makes them sensitive to specific shapes, contrasts, movements, or even color appearances of the visual input (Bowmaker, 2002).

After that, visual information is then transmitted to the optical neuronal pathway. The axons of the ganglion cells are thin and are not myelinated (*myelination*: a lipid rich surrounding of the cells for electrically insulation) in the intraocular part of the eye to guarantee transparency of the fibers (Miyake et al., 2004). They exit the eye at the *optic disc*, an area without photoreceptor cells and entry point for the blood vessels that supply the retina. As there are no photoreceptors, the optic disc is also referred as the “blind spot” of the eye, but because of interpolation of surrounding information and a constant optic flow caused by eye movements, this blind spot is not noticed in daily life.

After the exit of the axons of the ganglion cells at the optic disc, they form the *optic nerve*. In the extraocular part, the optic nerve fibers are myelinated (i.e., as an insulation of the electrical signals to guarantee rapidness and preservation of the signal). The optic nerve extends through to the *optic chiasm*, in which the signals from both eyes are sorted and combined via a partial crossing (decussation) of the nerve fibers: Fibers from the nasal half of one eye cross the midline and join fibers originating from the temporal half of the other eye (Derrington, 2002). This crossing allows information from the same visual field (e.g., right nasal visual field and left temporal visual field) to arrive in the same brain regions. Because of combination and superimposing of the images that

are originating from different retinal areas of both eyes, a binocular picture can be generated. This is the basis for stereopsis, the ability to perceive depth and three-dimensional pictures. The amount of decussation of the optic nerve fibers at the optic chiasm varies depending on the position of the eyes: Whereas for animals with laterally placed eyes (most prey animals) there is almost a complete decussation (> 65%), there is less crossover (50%–65%) in animals with frontally placed eyes (most predator animals; Herron et al., 1978).

After the “mixture” of the fibers, these proceed as the *optic tract* to the LGN in the thalamus. The LGN is the relay center of the visual information before the information proceeds to the primary visual cortex. It is divided into several cell layers from which some are receiving input from the large ganglion cells (M, alpha, or Y ganglion cells) and some from the small ganglion cells (P, beta, or X cells). Neighboring cells and cell layers are thereby receiving input from corresponding retinal fields of both eyes; that is, the same information is kept together (topographical mapping; Wolfe et al., 2010). However, in the LGN no reorganization of the retinal signals happens, so the receptive fields of the LGN cells mirror their retinal inputs (Derrington, 2002). The organization of the LGN differs between species, but it is commonly agreed that human, monkey, cat, and dog LGNs consist of six layers or sublayers (Casagrande & Norton, 1991). In nocturnal animals, the lateral geniculate body further contains the *medial interlaminar nucleus*, which is responsible for dim-light vision.

Further the optic tract extends to the *pretectal area* in the midbrain, which is responsible for feedback to the nerve fibers and muscles in the eye to initiate pupillary light reflex, optokinetic motor responses (fast and reflexive eye movements to keep a moving object stable on the retina), and accommodation reflex (synchronous accommodation of both pupils to an unilateral stimulus).

From the LGN the nerve fibers are subsequently passed via the *optic radiation* to the *primary visual cortex* (V1) in the occipital lobe of the brain. The primary visual cortex is again organized in several layers and sublayers and is characterized by topographical mapping so that neighboring information stays together. Input from the LGN is predominantly processed in the fourth layer of the V1 (Wolfe et al., 2010). An important feature of the V1 is cortical magnification: Information originating from small retinal ganglion cells will be “magnified” because of processing in a large area of the V1, whereas information originating from large retinal ganglion cells will be processed only by a small part of the V1. The

cortical magnification is therefore important for the high resolution in the point of focus. In the V1, each cell receives input from several retinal ganglion cells, and the receptive fields are therefore pooled together. Hence, they are arranged such that they are sensitive to specific conditions of the visual input. Therefore, at this stage they can be selective for color gradation, orientation, and direction of the visual input.

The stream of the visual information then passes to the V2 (one layer of the secondary visual cortex) and will subsequently be distributed into two streams: the dorsal stream passing the V3 and V5 sending information to the parietal lobe, and the ventral stream passing the V3 and V4 sending information to the temporal lobe. The dorsal stream controls visual actions and is commonly referred as the “where” pathway; visual areas in this stream are responsible for motion, object representation in space, and the control of extremities. The ventral stream is the “what” pathway and associated with color, form, and object recognition. Note that this is of course a simplified embodiment, but a detailed listing of the functions and functionality of the visual cortex is beyond this review (for further reading, see Kolb & Whishaw 2014; Roberts, 2002; Wolfe et al., 2010).

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