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Review Article

What Horses and Humans See: A Comparative Review

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Adaptations of the mammalian eye have tailored each to its own particular ecological niche. On the one hand, it would appear that the horse is best served by a system that can keep "half an eye" on everything, while the human benefits from focussing on more specific aspects of the visual array. By adapting a range of techniques, originally used to assess human visual ability, it has been possible to compare the human visual experience with that of the horse. In general, the results of the majority of these comparative studies indicate that the visual capabilities of the horse are broadly inferior to the human equivalents in acuity, accommodation, and colour vision. However, both the horse and human abilities to judge distance and depth perception may be quite comparable while equine vision is certainly superior to that of human's under scotopic conditions. Individual variation in visual ability, which is routinely taken for granted in humans, is also likely to occur in the horse. Such variation would undoubtedly affect equine performance, particularly in terms of expectation of athletic competitive outcomes in modern equitation. In addition to such considerations as conformation and athletic ability, a detailed assessment of the visual ability might contribute to a more accurate prediction of future performance characteristics in the horse. Although further investigation is required in order to appreciate fully both the capabilities and limitations of the equine visual system, the information currently available should now be considered and applied more rigorously both in the design of the equine environment and in the implementation of contemporary equine training methods. This need is the greatest in areas of equestrian sport where the outcomes of either or both equine and human visual judgements can be critical, the cost of failure often high and occasionally results in fatal consequences for both parties of the horse-human dyad.

1. Introduction

Historically there has been much discussion and debate as to the visual ability of the horse (*Equus caballus*). In the earliest known work on the horse, written twenty three centuries ago, Xenophon links the possession of a prominent eye with the ability of the horse to see over great distances [1]. More recently but still over half a century ago, Walls [2] reported that horses appeared to enjoy excellent vision based upon Arab legend concerning the ability of the Arabian horse to recognise their masters from afar. Shortly thereafter, a more scientific approach to the assessment of equine visual ability was adopted by Grzimek [3] who also later pioneered a number of studies into other aspects of equine behaviour [3]. Further advances in methodology and technology have resulted in additional conclusive findings, but the value of the early work should not be underestimated. For example, despite a series of inconsistent findings [3–6], the most recent investigation into colour vision in the horse has largely substantiated Grzimek's early work [7, 8].

A number of different methods are now used to investigate visual perception in animals where the structure and adaptations of the eye provide the initial evidence of "potential visual capabilities" within any species. Thereafter any theories regarding such potential visual capability then need to be demonstrated behaviourally in order to confirm or refute the predictions made. The amount of information available had been limited, at least in some considerable part by, not only design features of the various experimental protocols, but also the time it takes to conduct such behavioural trials [9]. However, a number of recently developed techniques have been shown to produce consistent results and will allow more accurate predictions to be made in the future. One of our objectives here is to evaluate the correlations found between the different approaches used when assessing equine vision and then subsequently to highlight the areas that warrant further investigation.

The horse is unique with respect to its relationship with humans. Although this close partnership may have resulted in a number of misconceptions in relation to the visual ability of the horse [10] it also means that there is a requirement to find out more. While it may never be possible to view the world through the eyes of a horse, by comparing aspects of equine and human vision, the similarities and differences can be explored. This is particularly relevant during ridden work when two separate visual systems have to coordinate and control what is essentially one pattern of movement such that any resultant athletic performance is the consequence of two different perceptual experiences. A further objective of this review is thus to compare equine and human vision and to identify visual features that are salient to either the horse or the human, or to both. The adaptations of the equine visual system will be compared to human visual perception and the application of these findings to ridden work will be discussed. Although the ultimate aim should be to gather together enough information to allow an appreciation of the overall visual experience of the horse, such a goal is still some way off.

2. Adaptations of the Equine Visual System

The equine visual system displays adaptations to particular environmental conditions, accentuating those features that are most important for the survival of this herbivorous prey species. Feral horses spend approximately 50–60% of their time grazing with their heads lowered and their eyes near ground level [11]. The horse's requirement for large amounts of fibrous herbage [12], and the open grassland that provides this, leaves the horse vulnerable to predation. The horse is subject to little or no threat from aerial predation, and typically, predators include wolves, lions, and snakes such that ground level visual stimuli are particularly salient to the horse. Furthermore the risk of predation is not limited to daylight hours and, similar to the larger carnivores and some other ungulates (e.g., cows and sheep); the horse is active during both the day and night. Although feeding activity in the horse has been found to occur throughout the day and night, this activity peaks after dawn and before dusk [11]. Therefore this crepuscular lifestyle requires a visual system that is sensitive in low light levels (scotopic conditions), provides early warning of approaching predators, and can assess the immediate ground conditions quickly for a speedy escape from imminent danger.

3. The Visual Field

The position of the equine eye and resultant visual field varies greatly from that of the human. The frontally placed human eyes convey a number of advantages where each eye has a visual field of approximately 150° with a large degree of binocular overlap. The consequence of receiving similar visual information from two eyes simultaneously is to increase visual acuity (the ability to see detail) and to provide information about the distance and solidity of objects [13, 14]. The position of the human eye also means that visual attention will be focussed on stimuli that are positioned directly ahead. In contrast, the lateral position of the equine eye provides the horse with almost panoramic vision, which facilitates maximum detection of predators at the expense of the advantages of binocular overlap.

The equine eye is large and prominent, being housed within enclosed orbits located laterally in the skull [15]. Together with the size and curvature of the cornea, size and horizontal shape of the pupil, and angular extent of the retina, this provides the horse with extensive monocular vision. In particular, from an anatomical perspective, a marked forward prolongation of the nasal retina provides the horse with a wide visual field [16]. The retinal field of view of each eye in the vertical plane has been estimated (using measurements based on the position and dimensions of the equine eye) at 178° [17], while that in the horizontal plane is slightly greater at approximately 200° [18]. Furthermore, the elongated horizontal pupil also allows much wider lateral vision than is possible with the circular pupil of the human eye [19].

The binocular overlap of the visual field is located down the nose of the horse and is limited to between approximately 65° [16] and 80° [18]. Two blind spots have been identified within the equine visual field, one in front of the forehead [18, 19] and one directly behind the horse [19]. It has been noted that variations in the settings of the eyes and head carriage, which are characteristics of different horse breeds, can affect the extent of these blind spots [20]. In breeds of horses where the mane, in particular in the region of the forelock, is long and thick, vision may also be affected, Figure 1. However, given the length and mobility of the neck, the horse can bring such areas into view quickly. With the head lowered, the horse has the benefit of being able to scan the lateral horizon for potential threats with its monocular fields, while assessing the ground surface for both suitable food and safe footing with its binocular field [18]. Hanggi [21] reported that horses possess interocular transfer where stimuli seen with one eye are also recognised by the other eye.

Although relative to body size some mammals possess larger eyes than the horse, in absolute dimensions, the eyes of the horse are the largest [22]. Total eye volume has been reported in the ranges 45–50.9 mL [23] and 42–62.5 mL [24] and the variation does not appear to differ as a function of the breed of horse [24]. Andersen and Munk [25] reported that, in addition to such large internal space within the eye, the circumference of the equine retina was greater than that found in the eye of even the much larger bowhead whale. The large globe size and extensive retinal surface ultimately result in an image magnification that is 50% greater than in the human eye [26]. Clearly, this point should be taken into consideration when features of the retinal structure are used to make predictions about the visual acuity of the horse.

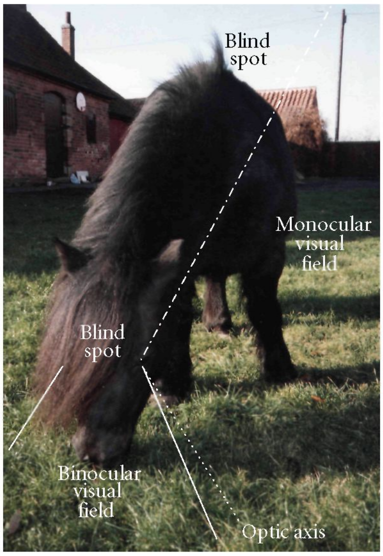

Figure 1: The position and extent of the binocular overlap in the region of the inferior visual field of the horse (approx. 65°: [16]). The extent of the monocular visual field, blind spots, and angle of the optic axis (approximately 40° from the midline: [15]) are also shown.

4. Accommodation: The Ability of the Eye to Focus

The refraction required to focus an image on the retina depends upon the curvature of the optical surfaces (cornea and lens), optical media, and the thickness of the optical component. In both the horse and human, the anterior surface of the cornea represents the primary ocular refractive surface [19, 27]. More precise focusing is the result of slight changes in the shape of the lens in response to the relaxation and contraction of the ciliary body, resulting in changes in the refractive power of the lens. This mechanism serves to maintain a focussed image of objects viewed from different distances and is termed accommodation [27].

Previously, horses were thought to lack this dynamic lenticular accommodation ability [28]. Indeed there is still some support in modern veterinary textbooks for the unique "ramp retina" theory previously attributed to equines. This theory assumed that the distance from the lens to the retina was variable with the dorsal retina being further from the lens than more central regions. Static accommodation occurred as a result of the image being focused on different areas of the retina, as brought about by changes in the angle of the head of the horse. Walls [2] and Duke-Elder [29] suggested that there was no evidence to support the occurrence of lens-adjusted accommodation in studies conducted on equine subjects. However, it has since been demonstrated that the equine lens is capable of limited accommodation [18, 30] and that only a small magnitude of change in refraction (less than 2 diopters) is required to maintain a focused image on the retina [30]. The movements of the head that were previously associated with the "ramp retina theory" in the horse have now been linked to the utilisation of the equine binocular field [18].

Essentially, the focal point must correspond to the retina in order to perceive a clear image. When this occurs it is termed emmetropia, and failure of the eye to locate the focal point on the retina is the consequence of refractive error. Human subjects can experience two forms of refractive error, hyperopia and myopia. In hyperopia the focal point is posterior to the retina and in order to bring images into focus the refractive power of the eye must be increased. This is accomplished by continuous accommodation, which if sufficient, will result in a clear focused image. However, such uncorrected hyperopia will often result in eyestrain and sometimes headaches [27]. Less accommodation is required to view objects in the distance than those close nearby and during myopia the focal point is anterior to the retina such that the objects viewed from nearby are seen most clearly. In humans, it has been estimated that approximately one in five people is myopic, while one in three is hyperopic. However, it is now also known that the incidence of both hyperopia and myopia varies considerably in relation to age, race, and geographical location [27]. Many common daily visual demands of the human lifestyle require adjustments of refractive errors in order to optimise performance in routine tasks such as, for example, reading and driving a car.

The horse does not appear to exhibit significant refractive errors, but there is a tendency towards hyperopia [22, 26]. Calculations, based on the equine eye being a general lens system, were made in one study of the physical optics of the equine eye. The eyes of three mature horses were assessed and they were all found to be hyperopic [22] and therefore based on their findings, Knill et al. [22] concluded that the horse should have excellent visual acuity for distant objects. Farrall and Handscombe [26] assessed the refractive errors of 30 eyes (from 15 horses) and found 7 eyes to be myopic, 10 were emmetropic, and 13 were hyperopic.

The ability to see distant objects most clearly is an obvious advantage to prey species and it has been noted that many wild mammals tend towards hyperopia [31] and so it is indeed likely that the Arabian horses could easily recognise their masters from afar [2]. It is also likely that horses, like many other mammalian species, may experience difficulty in focussing on objects less than 1 metre away [18, 20]. As in other domestic species there is some evidence to suggest that domestication and, perhaps inappropriate stabling in particular, have had the effect of altering the hyperopic vision in the horse and inducing a situation of equine myopia as a consequence [22, 31]. However, Harman et al. [18] failed to find any evidence of this development in the horses used in their study.

Another factor that should be considered, when assessing the ability of the horse to focus on images at different distances, is the size of the aperture (the pupil) through which the light passes into the eye. In general, the smaller the aperture, the greater the range of distances that will appear focused, and as the pupil size decreases, the depth of focus increases [32]. The human pupil can alter in diameter and attain the optimum size for resolution of 2.0 millimetres [33]. However, in the horse, the horizontal pupil while allowing the horse a wide visual field, does not enhance resolution. In fact, the size of the horizontal pupil is reduced by relatively weak circular muscles [15], which limits the depth of focus available to the horse. Consequently, it is thus extremely likely that while the horse may be able to focus on specific images, other areas of the visual array will appear more blurred.

5. The Perception of Depth and Distance

The frontal placement of human eyes, while limiting the overall field of vision, provides the advantage of a wider range of binocular overlap. Stereopsis is the ability to see depth based on binocular disparity, and it has been cited as one of the more beneficial advantages associated with frontal eye placement [2]. However, notwithstanding the lateral placement of their eyes, it has also been demonstrated that horses enjoy a full range of stereoscopic skills [34]. While equine stereopsis occurs within a limited field, it has also been shown that the horse can use other additional cues to judge depth [35]. In fact, physiological evidence supports the existence of stereopsis in other lateral-eyed animals as discussed by Hughes [17], and binocular neurons have been found in the cortices of a number of species, including the rabbit [17], goat [19], sheep [19], and guinea pig [36].

Timney and Keil [35] provided the first behavioural demonstration of a full range of stereoscopic skills in a lateral-eyed animal, the horse. The two horses in the study were trained to discriminate between stimuli on the basis of whether or not the target stimuli protruded from a screen (in other words either a 2-D image or 3-D image). The findings demonstrated that when the horses viewed the target stimuli binocularly, their performance was better than when the stimuli were viewed monocularly. In fact, depth measurements from the binocular thresholds were several times superior to those obtained monocularly and the authors concluded that horses would therefore use stereoscopic information preferentially when it was available [35]. In addition to the binocular overlap within the visual field, the horse has a relatively large interocular distance. Human subjects experienced an enhanced sensation of depth when the disparity of their retinal images increased and this has been cited as further evidence of depth perception in the horse [35, 37].

The horse has also been shown to be sensitive to pictorial depth cues [34]. The two horses in this study were trained to make a relative-line-length discrimination. They were able to distinguish between two lines reliably: a lower line 10 cm long from an upper line of 14 cm long when at a viewing distance of approximately 160 cm. Timney and Keil [34] also investigated whether horses were susceptible to a visual illusion, which was generated by pictorial depth information. During the experimental protocol, two lines of equal length were superimposed on a photograph of railway lines (presenting many pictorial cues to depth) and on a pastoral scene with much fewer depth cues and the horses overwhelmingly chose the railway track display. In human subjects, if two lines of equal length are superimposed on two flanking lines tilted inwards, the upper line looks longer than the lower line and is known as the Ponzo illusion. This effect is even greater during a situation such as if the lines are superimposed on a photograph containing perspective and other cues to depth. As in humans, the horses tested with the railway track photograph and pastoral scenes were found to be susceptible to the Ponzo illusion. Timney and Keil [34] concluded therefore that horses would utilize pictorial depth cues, as do human observers in similar situations.

The importance of the equine binocular portion of the visual field for judging distance was discussed by Harman et al. [18]. In order to direct this binocular portion forwards, the horse must be allowed to raise its head. This is of particular importance in equestrian competition such as jump racing or showjumping when the horse approaches obstacles/fences at speed. Both horse and rider must use and interpret visual information accurately in order to negotiate the obstacles/fences successfully. In a study by Laurent et al. [38], it was found that riders consistently focused their gaze centrally towards the top of the obstacle to be jumped. This suggests that the riders used the retinal expansion rate of the obstacle to assess the time to contact (takeoff point). Given the evidence that other animal species demonstrate an appreciation of size constancy [39, 40], the speed at which the size of an approaching object increases may also provide the horse with the means of judging distance. For both horse and rider, accuracy of takeoff would thus be enhanced by prior experience of approaching obstacles at varying speeds. However, if the speed of approach causes the retinal image to expand faster than can be processed by the horse or rider, mistakes are likely to occur in judging the distance from the obstacle and thus in assessing when to initiate takeoff.

The ability to utilize visual cues to assess spatial relationships between objects has been linked to head movements. In humans, when the head is moved from side to side objects that are viewed from different distances appear to change position relative to one another. Nearby objects are displaced to a greater extent than more distant ones and this information is utilized to make judgements about relative distances between them. This phenomenon is referred to as motion parallax and may occur as a result of eye movements in addition to movements of the whole head. Human vision has been shown to exploit such information in addition to binocular stereopsis in the judgement of depth [41, 42]. Motion parallax, as evoked by head movements, has been found to contribute to distance estimation and depth perception in insects and probably occurs in birds and rodents also. However, there is currently a lack of conclusive evidence for the role of head movements (or how head movements affect motion parallax) in larger mammals such as the horse [43].

As in a number of other species, including humans [44, 45], gender differences in visuospatial ability have been reported in the horse [46]. This ability has been defined as the mechanism by which an individual monitors changing spatial relationships that occur as they move through their environment [47]. Such changes are inevitably affected by the speed at which the movement occurs and the precise means by which they are monitored may vary as a result.

In all species investigated to date, including horses, males have exhibited superior visuospatial ability compared to females [45, 46] and this difference in visual ability may contribute to the relative success of male as compared to female horses [48, 49] at the highest level of competition. There is no evidence however as to which of the possible visual mechanisms responsible for the perception of depth and distance may be sex-linked. Further investigation is required in order to determine whether the ability to judge distance at speed varies between male and female horses, or indeed between male and female riders. Regardless of any potential differences, between males and females of either species, it is likely that the horse, being more familiar with travelling at speed than most humans, is better able to judge distance when approaching any obstacle rapidly than its human counterpart.

6. Visual Acuity

The ability of the eye to transmit detailed images depends upon the amount of information available from the retina and is clearly of particular importance in many human activities. The retina consists of an outer layer of photosensitive cells and an inner layer of nerve cells. Two main classes of photoreceptor are present (rods and cones) and both photoreceptor types synapse with bipolar cells, while these bipolar cells in turn synapse with retinal ganglion cells. The rods are responsible for vision in scotopic conditions, but because a large number (up to 45) synapse with each bipolar cell they provide poor spatial resolution compared to the cones [50]. The cones are less sensitive to low light levels, but result in better spatial resolution as a result of their neural connections—in the human fovea each will connect with a single bipolar cell. The cones also respond to light more quickly than the rods, resulting in improved temporal resolution [50]. This in essence is why the cones are responsible for vision during photopic (bright light) conditions.

As a result, an individual's visual acuity can be estimated by assessing the type of photoreceptors that are present, and their connections with bipolar cells, as well as the size and density (and, by implication, the receptive fields) of the retinal ganglion cells. Within the retina of the human eye, the central area of the fovea consists entirely of cones. As the number of cones decreases rapidly with increasing distance from the fovea, so at the same time do the numbers of rods increase rapidly [51]. Within the fovea, each retinal ganglion cell connects with a single photoreceptor [52] which ensures that this area is capable of the greatest acuity. Acuity varies to some degree in the human, but the limit of resolution of a normal observer lies between 50 and 60 cycles/degree [53]. Moreover this level of acuity is confined to the central region of the fovea, with values of between 35 and 40 cycles per degree attributed to the greater part of the visual field [54]. An area comparable to the human fovea exists in the retina of the equine eye. The distribution of retinal ganglion cells in the horse has been measured, and a streak of high cell density exists along a straight horizontal line, dorsal to the optic disc [55]. The cell density has consistently been found to be greatest at the temporal end of this visual streak [18, 55, 56], corresponding with the area responsible for binocular vision. The equine ganglion cells were found to be relatively small within the visual streak and of a fairly uniform size, whereas in the peripheral retina there was a mixture of all sizes of ganglion cells [55].

However, a number of different studies have produced conflicting evidence as to the visual acuity of the horse. François et al. [57] concluded that the horse would have poor vision, particularly under photopic conditions, as a result of the predominance of rods over cones in the entire retina. More recently Ehrenhofer et al. [58] reported the existence of large gaps between ganglion cells in most parts of the equine retina and that the majority of these ganglion cells were not only very large but they were also associated with many amacrine cells in turn. (Amacrine cells lack long fibrous processes). The speed of conduction (fast) of the axons of these large ganglion cells and their connections with the amacrine cells suggests that the horse would be particularly sensitive to subtle changes in illumination and stimulus motion. It is therefore, only in the area of the visual streak and a small area close to the optic disc (the area centralis) where there is a well-balanced ratio of photoreceptor, bipolar, and ganglion cells, that the horse possesses any real visual acuity [58].

In another study, anatomical data provided an estimate of peak visual acuity in the area of the visual streak of about 16.5 cycles/degree, with far lower acuity (3.3–3.5 cycles/degree) in other retinal regions [18]. This estimate is very similar to the 16.4 cycles/degree that was obtained in an earlier study by Hughes [17], but slightly higher than the best value of 12.3 cycles per degree obtained by Ver Hoeve et al. [59]. A behavioural study that focussed on visual acuity in the horse had resulted in a range of values, with the best acuity obtained being 23.3 cycles/degree and the lowest being 10.9 cycles/degree [60]. Individual variation in both the size (of the horse) and the horses' approach to the task was considered to be the cause of the variation in the Timney and Keil [60] behavioural study. Furthermore Evans and McGreevy [24] have just recently reported that ganglion cell density within the visual streak varied between different breeds of horse and that horse breeds with longer heads may have better visual acuity than those with shorter heads. A similar situation has been observed in dog breeds where a correlation has been found between nose length and ganglion cell distribution. A regular horizontal streak has been reported in long-nosed breeds (and in the wolf) whereas a strong area centralis with virtually no streak was found in short-nosed breeds such as the pug [20].

At this point in time, calculations of equine visual acuity, which have been based on both physiological and behavioural data, have produced some variable results. This may in part be the result of individual differences among horses, but it has been shown by Pesudovs et al. [61] that different methods of measuring visual acuity might actually generate different results too. It is also likely that results based on calculations of a single factor, such as retinal ganglion cell density, will be less accurate than when multiple visual mechanisms are considered. Despite these reservations, it is generally accepted that visual acuity in the horse, at least in photopic conditions, is poor in comparison with human vision. It is likely however that, perhaps unlike the human, the horse does not necessarily require the ability to see in great detail in a great many instances. Other less detailed visual attributes such as motion detection and an awareness of the surrounding environment may be far more important for the horse. On the other hand and as in the human, it is likely that visual acuity in the horse will vary to some degree according to a number of different factors such as breed, age, previous experience, and general health status. However, unlike the individual clinical routine assessments regularly conducted in humans, there has been no evaluation of how this visual ability varies in the horse, or indeed how such variation may relate to or influence athletic performance or participation within equestrian competition.

7. Scotopic Vision

Based on physiological data, [17] it is calculated that the horse, owl, dog, and grey squirrel have similar light collecting power even in spite of the difference in the size of their eyes. Furthermore, these values rank below those calculated for cat, rabbit, and rat based on the values recorded for maximum pupil diameter. Hughes [17] also contrasted both daylight and nocturnal vision characteristics between horses and humans and reported that while human daylight vision is most acute, nocturnal vision in the horse is superior to that in humans. As we have previously stated, horses like other herbivorous ungulates are active during both daylight hours and during darkness at night and their visual system has subsequently evolved to function in both scotopic and photopic conditions. However, even though equine retinae contain both rods and cones, the former outnumber the latter by approximately 20:1 [62], although within the area of the visual streak, a higher percentage of the photoreceptors (approx. 17%) were found to be cones [57]. Cone densities vary from approximately 5000 per square millimetre in the peripheral retina to 15 000–20 000 per square millimetre in the visual streak [63]. This is considerably lower than the mean peak density in the human fovea of 161 900 cones per square millimetre but comparable with the cone concentration found in the peripheral human retina where cone density has been measured as less than 5000 per square millimetre [51]. This is further supporting evidence that human visual ability is likely to be superior in photopic conditions, at least in the area of the fovea, whereas the horse is likely to have the visual advantage in scotopic conditions.

The ability of the horse to see in levels of low light is also enhanced by the presence of an intraocular reflecting structure, the tapetum lucidum [64]. This structure is present in species that are not strongly diurnal (e.g., carnivores, rodents, sheep, cows) and represents an adaptation for dealing with scotopic conditions. The tapetum lucidum increases retinal sensitivity by reflecting light back through the photoreceptor layer [64], but at the expense of resolution by the scattering of this light [55]. Moreover, the lower margin of the choroidal tapetum fibrosum of the horse coincides with the location of the visual streak [55]. It extends horizontally from the surface of the optic disc almost to the equator, and to a comparable distance above the optic disc, forming a rounded triangle in the upper half of the retina [64]. The position of this reflective layer provides a mechanism that increases sensitivity to light, particularly to that reflected from the ground [10] and in contrast to the forward-directed human gaze, ground level visual stimuli are therefore most salient to the horse [65, 66].

Thus the lifestyle of the horse is better served by visual sensitivity in low light levels at the expense of the ability to see objects in great detail. Light enters the equine eye through the horizontal pupil, which while allowing the horse a wide visual field, does not enhance resolution and is slow to adapt to differing light levels. The human pupil can alter in diameter in response to changes in the level of light and attain the optimum size for resolution of 2.0 millimetres [33]. Contraction of the circular muscles within the iris quickly reduces the size of the pupil in response to bright light, thus preventing damage to the light sensitive retina. In contrast, the size of the horizontal pupil of the horse is reduced by relatively weak circular muscles and adapts less quickly to changes in light levels [15]. To prevent actinic damage during grazing, the dorsal papillary margin has specialist projections (the corpora nigra), which act to shade the lower half of the retina and these projections are also thought to contribute to constriction of the pupil [23]. This adaptation, by limiting the extent to which light enters the eye from above, also serves to accentuate information from the inferior visual field. As a result, however, the horse is subsequently more easily “blinded” by exposure to sudden bright light. This presents practical difficulties for the horse when navigating between abrupt changes from dark to well lit areas (and vice versa) such as from shaded areas into bright sunlight and this is likely to have implications for certain aspects of equitation. Saslow [67] demonstrated that stimuli viewed in overcast, rather than sunny daylight conditions, are actually clearly visible to the horse. The external features of the equine eye (Figure 2) include the iris, which in terms of colour generally varies from dark brown to golden brown to yellow, occasionally blue or white [68]. While these features have provided beneficial adaptations to the horse in low light levels, the presence of cone photoreceptors in the equine retina and diurnal activity patterns would also suggest that the horse enjoys the benefit of colour vision.

8. Colour Vision

The perception of colour requires at least two spectrally different classes of receptor, together with neural pathways capable of comparing their output [69]. An animal is said to possess colour vision if it can discriminate between stimuli that differ in their distributions of spectral energy, independently of any differences in total energy [70]. The ability of the horse to perceive colours has been a matter of debate for quite some time and of the two main types of photoreceptor cell present in the retina of the horse, the

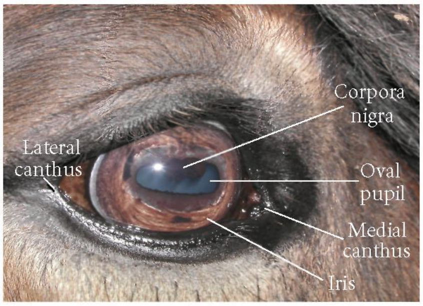

Figure 2: External features of the equine eye (right eye), including the horizontal pupil, corpora nigra, lateral and medial canthus (angle at either end of the eyelid aperture), and iris.

cones are responsible for both photopic vision and the ability to see colour [71]. Notwithstanding the array of inconsistent findings among behavioural studies [3–6] and the studies that have investigated the spectral sensitivity of the cone photopigments of the equine retina [8, 54, 59, 72–75], the overall and generally accepted conclusion is that the horse possesses, at least, a form of colour vision.

The most common form of mammalian colour vision is based on the possession of two cone types (dichromatic), one having maximum absorption in the short wavelength end of the spectrum, the other in the middle to long wavelengths [70]. In contrast, however, human colour vision (and that of Old World monkeys, apes, and one New World group, the howler monkey) is based on three cone types (trichromatic), with maximum absorption in the short, middle, and long wavelengths [76]. Values of approximately 420, 534, and 563 nm have been obtained for the spectral peaks of these three cone types in the human [77], although some individual variation in the long wavelength peak has also been reported [78]. Essentially, identification and classification (naming) of different colours relate to the appearance of the visible spectrum to these trichromatic humans. The specification of these colours is typically universal, with eleven named colours currently in common use in all fully developed languages for the labelling of surface colours [79, 80]. (The eleven named colours are as follows: red, orange, yellow, green, blue, purple, black, white, brown, grey, and pink [80].) A small percentage of the human population has defective colour vision and this so-called "colour blindness" is more common in males than females, with approximately two percent of the male population lacking one class of photopigment, resulting in dichromacy [81]. Human dichromacy results from the absence of one of the three cone photopigments such that individuals with defective vision are described technically as protanopes, deuteranopes and tritanopes. These individuals are lacking of long, middle, or short wavelength photopigments, respectively [82].

As a consequence, the perception of colour based on the output of only two types of cone photoreceptor results in the division of the visible spectrum into two hues, instead of the range of spectral colours perceived by the trichromat [83]. The perception of neutral colours (colours that are neither bright nor intense and have low saturation) is thought to be the same for both trichromats and dichromats [81], where the ratio of output from the different cone types results in an achromatic perceptual experience. This phenomenon is termed the neutral point and essentially divides the spectrum into the two hues as perceived by the dichromat [83]. The horse possesses at least two types of cone photopigment, one maximally sensitive to medium-long wavelengths, the other to short wavelengths and the horses is thus termed dichromatic. Values for the spectral peaks of these photopigments have been estimated at 545 nanometres (nm) [59, 72, 75]) and 429 nm [72]. These values vary slightly from those obtained by Campbell and Green [54], but they are both consistent with the range found in other ungulates [70]. The dichromatic neutral point has also been located in the horse at about 480 nm [84]. Behavioural evidence is then required in order to determine whether or not these findings are accurate predictors of the ability of the horse to actually perceive colour. The neutral point test has been used to assess colour vision in animals and evaluates the subject's ability to discriminate between equiluminant monochromatic and achromatic lights. The test essentially determines if there is a band of wavelengths at which an animal's performance drops to levels of chance alone.

Behavioural studies into the ability of animals to see colours have generally involved training the subjects to discriminate between chromatic and achromatic stimuli, where all other cues (in particular differences in lightness, olfactory, and spatial cues) have been controlled or typically made irrelevant. Until quite recently only four colours had been tested on the horse in this way, with inconsistent results [3–6]. Although all of these studies concluded that the horse had the ability to discriminate blue from grey, the results for red, green, and yellow were variable. For example, Grzimek [3] found that the horses in his study could discriminate yellow best, followed by green and then blue, but had some difficulty with red. The subjects tested by Pick et al. [4] could reliably discriminate blue and red from grey, but encountered difficulty with the colour green. Similar results were obtained by Macuda and Timney [5] whose horses could also discriminate blue and red from grey, but could not discriminate either green or yellow from the grey colour. Smith and Goldman [6] found some variation in the ability of the horses that they tested and although all the horses in this study successfully reached the criterion for learning (85% correct responses) with red and blue—one of the subjects performed at chance levels only for yellow and green.

One of most recent behavioural studies of colour vision in the horse [7] investigated the correlation between the predicted effect of various colours on the photopigments of the horse and their ability to discriminate the colours from grey colours. Using the values for the peak sensitivities of the cone photopigments of the horse (429 and 545 nm: [72]), the effect of fifteen colours from across the spectrum on the equine visual system was assessed using modelling techniques of Govardovskii et al. [85]. The findings indicated correlations between the predicted effect of the colour and the ability of the horse to discriminate the test colour from grey. The six horses used in the study were able to use chromatic information across the spectrum, including those wavelengths that would be perceived as green and yellow. The colours orange, yellow, and blue were the colours that the horses most easily discriminated from grey—as was consistent with the predictions made [7]. Moreover as was the case with Grzimek [3], Hall et al. [7] also found that the horses actually failed to discriminate the colour red as easily as they discriminated the other colours from the grey control. In more recent studies with respect to equine colour vision [8, 73], the authors have also concluded that horses appear to have dichromatic capability only, much like the red-green colour deficiencies found in some humans.

Based on a synthesis of all the work to date, it would appear that the ability of the horse to perceive colours may be somewhat comparable to that of human dichromats. Although wavelengths from across the spectrum are likely to be perceived by the horse as coloured (apart from that at the neutral point) these colours will be seen as variations of only two main hues. In essence, the horse would fail to discriminate between colours that lie on the same side of the neutral point—at least this will not be possible on the basis of wavelength information. Similarly human dichromats commonly confuse reds and greens and fail to detect particular dot patterns comprising of these colours in simple "colour blindness" tests using Isihara cards. Jameson and Hurvich [86] reported that human subjects, with such dichromatic vision, when asked to arrange colours according to their degrees of similarly would routinely include mixed reds and greens in their chosen sequences. It now seems likely that the horse would experience similar differentiation difficulties, in particular with the colours lime green and orange, and, equally likely, with the colours blue and purple [7], although this phenomenon has yet to be conclusively tested or demonstrated in behavioural experimental work in the horse.

In addition and despite differences in colour perception, visual acuity in both the horse and the human appear to vary according to the colour of the actual stimulus. For example, Grzimek [3] found that equine acuity with blue targets was poorer than with other colours, including yellow. Although the horse could detect a perpendicular yellow line 5 millimetres wide from a distance of 3.3 metres (visual angle of $3'15''$ and equivalent to 18.46 cycles per degree), a blue line had to be 20 millimetres wide to facilitate detection from the same distance (visual angle of $20'41''$ and equivalent to 2.9 cycles per degree). The most plausible explanation for this difference in equine acuity is the low population of short wavelength photoreceptors within the visual streak of the horse including the irregular spacings associated with them [63]. Indeed, Harman et al. [18] concluded that the equine visual acuity value obtained for blue stimuli corresponded closely to that obtained for the peripheral retina (2.7 cycles per degree), while the values recorded for the yellow equivalent were closer to the value obtained for the visual streak (16.5 cycles per degree). A similar finding has been reported in relation to the human retina, where foveal tritanopia (absence of short wavelength cones) and the spatial distribution of these short-wavelength cones in the rest of the retina also have the effect of limited resolution with short-wavelength colours [87].

It should be noted, however, that while trichromatic colour vision allows greater discrimination of a greater range of colours, there are also certain visual advantages associated with dichromacy. Whereas colour generally enhances the visibility of objects, in some cases it may actually obscure differences between objects that are based on other features. Although human trichromats cannot detect objects that differ in texture once camouflaged by variegated colours, any such colour camouflage does not reduce their visibility to dichromats [88]. Thus, it may well be that certain objects may actually be more visible to the horse than to the trichromatic human—at least in some instances. Within the sport of horse-trials, for example, where most cross-country fences are often of a similar colour to their immediate surroundings, the ease with which the majority of horses negotiate such obstacles would suggest that the fences are clearly visible and readily interpreted by the equine visual system. This would suggest that the horse probably relies less on colour and more on other visual features such as textural differences to distinguish such objects from their surrounding environments.

9. Visual Perception and Performance in Equitation

Regardless of the differences between equine and human visual perception, this modality is of prime importance to both species. Behavioural observations of feral horses would suggest that visual cues are highly important in the recognition of other herd members [89]. During reproductive behaviour and when assessing whether a mare is in oestrus and ready to cover, mature stallions utilize visual stimuli to a greater extent than olfactory cues [90]. Indeed visual recognition of offspring by the mare is also important and the mare typically remains in visual contact with the foal for at least six months following parturition [91]. Furthermore, it seems certain that the dam can identify the foal visually from distances of approximately ten metres [92]. Among groups of adult horses, at least, visual information appears to be very important for recognition and in determining behavioural responses to other individuals.

The importance of understanding how the horse perceives the world becomes clearly significant within equitation where both the horse and human are working together (ridden, driven, or handling situations). Any failure on the part of the handler to appreciate the differences between equine and human visual experience may result in the misinterpretation of visual raw data on the part of the horse, which could then lead to inappropriate behaviour with undesirable consequences. For example, a horse that throws its head up and down when approaching a fence may well be struggling to see the obstacle, rather than trying to go faster or "misbehaving" or exhibiting other forms of conflict behaviour. Similarly any differences in colour perception between horse and human could easily result in situations where some individual colours that appear bright to human visual systems may be linked to adverse and undesirable reactions in the horse or vice versa. The colour red, for example, will appear less noticeable to the horse, while small movements (that may be imperceptible to humans) are much more likely than other visual features, such as colour, to elicit an avoidance response in the horse. In the same way there has been a longstanding but fallacious belief in relation to bullfighting that the bull reacts aggressively in response to the red cape. It has long been proven, however, that the movement of the bullfighter's cape is the primary cause of this response [93]. Equally, other similar misinterpretations of equine behaviour and colour vision are also commonplace.

When moving, both humans and horses use several aspects of visual information to negotiate and avoid collisions with obstacles within the immediate environment. Although Saslow [10] has suggested that horses might actually rely on senses other than vision primarily during some activities, vision is certainly of paramount importance when the horse is galloping and jumping at speed. There have been several anecdotal reports of horses with unilateral eye injury appearing to have less visual information available from the remaining visual field, particularly when negotiating enclosed or confined areas at speed. In one such set of circumstances, while a horse with unilateral eye injury was loose schooled within the outer confines of an indoor riding arena, there was no apparent alteration in kinematic behaviour while the injured eye was oriented towards the inside of the direction of travel. However, when the horse was galloping in the opposite direction (with the injured eye towards the outside), the horse was forced to slow considerably in order to negotiate the turns at the ends of the arena (Somers, personal communication). Similar adjustments in motor behaviour have been recorded in experimental studies of horses that were performing jumping trials under conditions where unilateral visual information was controlled by a specifically modified visor or blindfold apparatus [94]. The clear indication from such studies is that the visual information about the position of boundaries is important to the horse when moving at speed in a restricted space.

10. Vision and Jumping Kinematics within Equitation

During ridden work, certain disciplines of equitation and riding styles advocate the adoption of unnatural positioning of the head and neck of the horse. Although flexion of the neck (bending in various directions) may result in improved movement of the equine back [95], there may be much less advantageous outcomes for equine vision as a consequence [96]. Under conditions of extreme poll flexion, although the horse would still be able to see the ground, the area directly ahead is certainly obscured. In these situations, the ridden horse is then dependent upon the rider for directional guidance and is in effect working "blind" [20]. Harman et al. [18] declared that when approaching a fence, the horse should be allowed to alter the angle of its head and neck to optimise the assessment of depth and distance and thus affect takeoff in the correct place. It is fairly common for the ridden horse (when working "on the bit") to be subjected to visual restriction in some form and any such restriction of head and neck movements, either by the use of equipment or directly by rider intervention, may have the effect of limiting the visual information available to the horse. These restrictions of the equine visual system may affect the horse in ways in which we are as yet unaware and their impact not only on athletic performance but also on equine welfare warrants further detailed investigation.

Stachurska et al. [97] assessed the kinematic motor behaviour of horses when jumping a variety of different obstacles and increases in the height of the fence resulted in more frequent knockdowns. Stachurska et al. [97] also reported that horses exhibited refusals and "runouts" when approaching walls and that the second elements of combination fences (two or three related fences) prove more problematic than the first or third obstacle of combination fences. Moreover, fences with only a single colour (in particular, white) also caused more difficulties for jumping horses than those fences displaying two contrasting colours. Horses also appear to demonstrate more problems when negotiating fences of contrasting colours where green is paired with yellow or blue, which are two of the colours that have been reported as most easily visible to the horse [7]. Since to date it has not been possible to separate rider influences from these apparent visual shortcomings in the performance horse, such problems could also be the consequence of the human visual perception rather than that of the horse or some combination of both. Recently, eye movements in humans have been studied to identify the visual features that are important in the performance of different tasks. In general, skilful performers learn particular visual fixation patterns that are required by the task undertaken [98]. Similarly, eye movements, gaze studies, and attempts at more sophisticated eye tracking studies in the horse have the potential to provide so much more elucidation regarding not only functional and behavioural but also interpretative characteristics of the equine visual system [9].

In terms of rider eye movements during equitation, Laurent et al. [38] reported that horse riders consistently focused their gaze centrally on the target obstacle during the intermediate and final approach strides. Furthermore, more experienced riders tended to deliver their focus towards the top of the target obstacles and also tended to maintain their head in a fixed position. This approach is regularly employed to train other less-experienced riders in terms of precision and accuracy with stride kinematics to optimise takeoff position from in front of fences during jump training. When technological advances are sufficient to permit the mapping of the eye movements of successful jumping horses (when approaching different obstacles), much more detail will be available to address our incomplete knowledge of the equine visual system. Furthermore, studies of this nature are likely to provide us with vital information that could be used in the selection and training of other horses for various specific disciplines of equitation.

Figure 3: Some fence designs may challenge not only the athletic prowess of the performance horse but also the visual capability of the animal, which may have safety implications for both horse and rider.

In addition, it may be possible to minimise dangerous falls of horses and riders so often seen in some equestrian sports [99] as a result of improved safety standards in equestrianism through more appropriate fence/obstacle design. The lateral placement of the equine eyes, horizontal pupil, and panoramic visual field [100], however, presents serious challenges in designing eye-tracking testing apparatus for the horse. Some scientists suggest that it might even prove virtually impossible to assess the direction that any horse is looking and even more difficult to judge exactly what visual feature is being fixated upon as the horses tend to keep "half an eye on everything" rather than focusing on specific targets [100]. Motor accuracy and precision when jumping requires adaptive behaviour on the part of the horse and it may take some specialist practice to develop the visual skill and locomotory coordination that is required for such activity.

In terms of jumping kinematics, a study by Visser et al. [101] indicated that personality traits of young horses, such as emotionality and reactivity, might be used to predict their subsequent performance as show-jumpers. While vision per se was not examined by Visser et al. [101], a link between personality and visual ability has been suggested in humans. In one personality study, Trevor-Roper [102] observed a tendency for many hyperopic individuals to be extroverted outdoor-type personalities while myopic individuals were much more inclined to be introspective and contemplative. While no such evidence exists for horses, it does suggest the possibility of links between some characteristics of vision, personality, and athletic or performance ability. The study of animal cognition and emotion has become increasingly more important in terms of our understanding of animal behavioural responses and performance-related issues [103]. Equine conformation, motor coordination, and athletic fitness are vital ingredients ultimately related to equine performance. Additionally, individual variations in visual ability are equally likely to be major contributory factors in determining the success or otherwise of competition horses within the elite echelons of the various disciplines of equitation. As with the selection of all desirable traits in animal breeding programmes, it would be advantageous to be able to test for features of visual ability that were related to performance and utilise these as part of the selection processes.

The aim of the standard ophthalmic examination currently carried out by veterinary surgeons is to identify any abnormalities of the eye that could result in visual disability. It does not however take account of any individual differences (acuity, colour vision, depth perception) in terms of overall visual ability that could influence or contribute to the future success of the horse. Sex effects with respect to visuospatial ability have already been demonstrated in the horse [46]. As is the case in all other species investigated to date; male horses enjoy the benefit of superior visuospatial ability compared to female counterparts. There is an adaptive advantage associated with greater visuospatial ability in terms of depth perception, interpretation of three-dimensional perspective, and elements of navigation and visuospatial ability is likely to be critically important during the jumping phases of equestrian competition. Fence and obstacle designs within the various disciplines of equitation may well take account of the athletic ability of the horse, but the aesthetics and visual presentation of these structures are regularly based on human rather than equine visual perception and may cause difficulty and risk of injury for the horse (and rider) as a consequence, Figure 3. Fence designs that challenge not only the athletic prowess but also more importantly (and perhaps unfairly) test the visual ability of horses within equitation may contribute to the unacceptable levels of wastage and welfare concerns within equestrianism [104].

Within equine competitions, course and fence designs continue to diversify at the discretion of course designers who may not be aware of how these various elements actually appear to or are perceived by the horses that have to negotiate them. Some fence elements and fence designs have proven to be problematic for horses during the demands of competition [99]. The visual techniques and behavioural characteristics of successful competition horses should be considered when course designers attempt to create innovative course and fence designs for competitive equestrianism. Even outside of competition, while the information regarding what horses see is by no means complete, what is available should be considered more carefully when designing the various element's of the equine environment such that horses are not expected to see the world through the eyes of the human.

In one recent and very relevant study, the effect of different floor colours on the behaviour of the horse has been demonstrated [66] and this fundamental issue has implications for equine husbandry. For example, the impact of these findings in a routine management situation was then highlighted successfully by varying the colour of the matting on trailer ramps. Horses are regularly required to load into transport systems such as trailers or floats and the evidence now suggests that horses loaded more easily and without hesitation when the ramp mats were green compared to loading attempts when the ramps were covered with the more commonly used black matting [105]. For the most part, the environments in which horses are maintained are designed and constructed with human visual perception (including aesthetics and limitations) as the basis for how things should look and be presented to the horse. This strategy may be inherently flawed, but by also attempting to view the world through the eyes of the horse, much more appropriate environmental infrastructure might be possible as a result, which would lead to improved conditions in terms of equine husbandry, welfare, and performance within equitation.

11. Conclusion

Although there is a growing body of information relating to the capabilities and limitations of equine vision, the overall picture is still far from complete. Useful comparisons with specific features of human visual ability have been made, generally by adapting techniques that have been developed to assess human visual perception. While we can assess the visual ability of the horse using these parameters, little is known about other features that are not an important part of the human visual experience. The horse may respond to certain visual stimuli that the human eye even fails to notice, which would suggest that some visual capabilities of the horse, at least, may be superior to our own. Given the importance (and demands for accuracy and precision) of contemporary equitation, there is also a lack of information regarding individual differences in the visual ability of different horses and how this may affect any individual horse's athletic performance. Clearly, the development of more comprehensive methods that are capable of deciphering the complete extent of the equine visual system is warranted and would assist equestrians to optimise performance in the athletic or competition horse. A better understanding of the visual strategies employed by successful horses might prove extremely useful too when designing specific "schooling" routines that could assist in the training of the less-experienced horse. In terms of equine competition within the various disciplines of equitation, every effort should be made to reduce the risks associated with the various sporting activities that involve elements of motor accuracy, jumping kinematics, and speed by ensuring that the horse can "see" what is expected of it. In the high-end competition horse, this need is paramount given the athletic (including visual) challenges set by humans as they expose these horses to many potential risks associated with participation in the equestrian sports.

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