Equine Vision – A review of current knowledge and how it affects our relationship with the horse in terms of learning

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Abstract

Despite significant research in the field of equine learning behaviours and the fact that the relationship between humans and horses relies heavily on training, our knowledge of the cognitive abilities of equids remains limited. Researchers have identified two main factors that are indispensable for the better understanding of equine learning: the anatomy and physiology of the equine visual system and the discrimination and categorisation of stimuli by equids. The equine eye has very specific anatomical characteristics that have evolved significantly over the centuries in order to adapt to its environment. The influence of the herd behaviour as well as the primary flight response of equids has also played a major role in the development of their visual system. The adaptations of the equine eye allow them to, for example, recognize threats while grazing by maximizing the field of vision, depth perception and visual acuity from that physical position. Recent data on the functional anatomy of the eye has allowed for more accurate interpretation of previous studies on equine learning and the performance of visual tasks. Limitations to the study of equine behaviour remain, however, evidence of the detailed retinal structure and the time required to train horses for carrying out these studies reliably. Current evidence has established that stimulus position as well as size, colour and level of brightness have significant effects on equine visual acuity. This knowledge needs to be expanded upon as well as consistently applied both in the interpretation of existing evidence and in the design and implementation of new studies. A thorough knowledge of the horse's visual system is necessary for understanding, interpreting and, above all, improving interactions with the equine species, regardless of the discipline practised and further studies are necessary to improve our understanding of equine learning behaviours.

Abstract

Trotz umfangreicher Forschungsarbeiten auf dem Gebiet des Lernverhaltens von Pferden und der Tatsache, dass die Beziehung zwischen Mensch und Pferd in hohem Masse vom Training abhängt, ist unser Wissen über die kognitiven Fähigkeiten von Pferden nach wie vor begrenzt. Forscher haben zwei Hauptfaktoren ermittelt, die für ein besseres Verständnis des Lernverhaltens von Pferden unerlässlich sind: die Anatomie und Physiologie des visuellen Systems von Pferden sowie die Unterscheidung und Kategorisierung von Reizen durch Pferde. Das Auge des Pferdes hat sehr spezifische anatomische Merkmale, die sich im Laufe der Jahrhunderte erheblich weiterentwickelt haben, um sich an seine Umgebung anzupassen. Der Einfluss des Herdenverhaltens sowie die primäre Fluchtreaktion von Pferden haben ebenfalls eine wichtige Rolle bei der Entwicklung ihres Sehsystems gespielt. Die Anpassungen des Pferdeauges ermöglichen es ihnen beispielsweise, Bedrohungen beim Grasen zu erkennen, indem sie das Sichtfeld, die Tiefenwahrnehmung und die Sehschärfe aus dieser physischen Position heraus maximieren. Neuere Daten über die funktionelle Anatomie des Auges haben eine genauere Interpretation früherer Studien über das Lernen von Pferden und die Ausführung von Sehaufgaben ermöglicht. Die Untersuchung des Verhaltens von Pferden stösst jedoch nach wie vor an ihre Grenzen, da die Netzhautstruktur sehr detailliert ist und die Ausbildung der Pferde für die zuverlässige Durchführung dieser Studien viel Zeit erfordert. Derzeit ist erwiesen, dass die Position des Reizes sowie Grösse, Farbe und Helligkeit signifikante Auswirkungen auf die Sehschärfe von Pferden haben. Dieses Wissen muss erweitert und sowohl bei der Interpretation vorhandener Erkenntnisse als auch bei der Konzeption und Durchführung neuer Studien konsequent angewendet werden. Eine gründliche Kenntnis des visuellen Systems des Pferdes ist für das Verständnis, die Interpretation und vor allem für die Verbesserung der Interaktionen mit der Spezies Pferd notwendig, unabhängig von der ausgeübten Disziplin, und es sind weitere Studien erforderlich, um unser Verständnis des Lernverhaltens von Pferden zu verbessern.

Introduction

Behaviourists working in the equine field (1) provide a comprehensive account of equine learning behaviour, evaluating the evidence from a wide range of studies. Throughout their reviews, they emphasise the importance of identifying the horse's natural abilities with the ultimate aim of optimising the training of this domestic species. It is clear that, although the success of the horse-human relationship depends largely on training, our knowledge of the cognitive abilities of this species is very limited. Given the role of the horse as an elite athlete and developments in other fields, for example in equine assisted therapy, a better understanding of the factors that influence learning in this species is desperately needed. In particular, behaviourists (1) have identified two factors that are essential to our understanding of the processes involved in equine learning. The first is the need for further study of the equine visual system and the effect of the characteristics of this system on information acquisition and response to the environment. The second is the identification of the stimuli that are most important to the horse and therefore attract the most attention. To optimise training, it is important that the animal directs its attention to relevant signals and ignores irrelevant ones. Using our knowledge of the characteristics of the equine visual system, it is possible to present stimuli in a way that is most likely to be noticed by the horse. The question of what attracts the horse’s attention can therefore be answered, at least in part, by a better understanding of its visual perception. In this literature review, the link between the horse’s visual system and its learning ability will be explored, as well as the behavioural adaptations that may have an impact on cognition.

Equine vision and anatomy

Horse's eyes have very specific anatomical characteristics. The phylogenetic evolution of equids has been significant and their size and many of their organs have evolved greatly over the centuries. The equine eye is an organ that has adapted extremely well to its environment, which is mostly arid steppe. The influence of the herd behaviour of equids and the primary flight reaction has also played a major role in the development of the equine visual system.

There are many anatomical similarities between the human and equine eye, such as conjunctiva, cornea, lens, retina, optic nerve, aqueous and vitreous chambers (2). In veterinary medicine, it is important to monitor and treat the ocular health of horses as necessary. The eye is examined in a similar way as in human medicine, initially with a conventional ophthalmoscope (Figure 1) and then through evaluation of the integrity of the corneal surface using a fluorescein strip (Figure 2). The main differences of the equid eye are the oval shape of the eyeball, the presence of a third eyelid, which is necessary for adequate lubrication of the cornea at full speed (Figure 3), and the presence of iridic granules (corpora nigra) above and below the pupil, which have been the subject of much speculation and whose function is not entirely clear. Scientists attribute a function of appreciation of light intensity to them. The oval, horizontally oriented shape of the pupil allows horses to have a nearly complete view of their surroundings while grazing (Figure 4). The anatomical structures discussed above are presented photographically and in a schematic drawing in Figures 5 and 6. Horses have

Figure 1: *As in human medicine, the examination of the horse's eye is carried out using a conventional ophthalmoscope. Sedation is usually unnecessary.*
Source: *Dr Montavon*

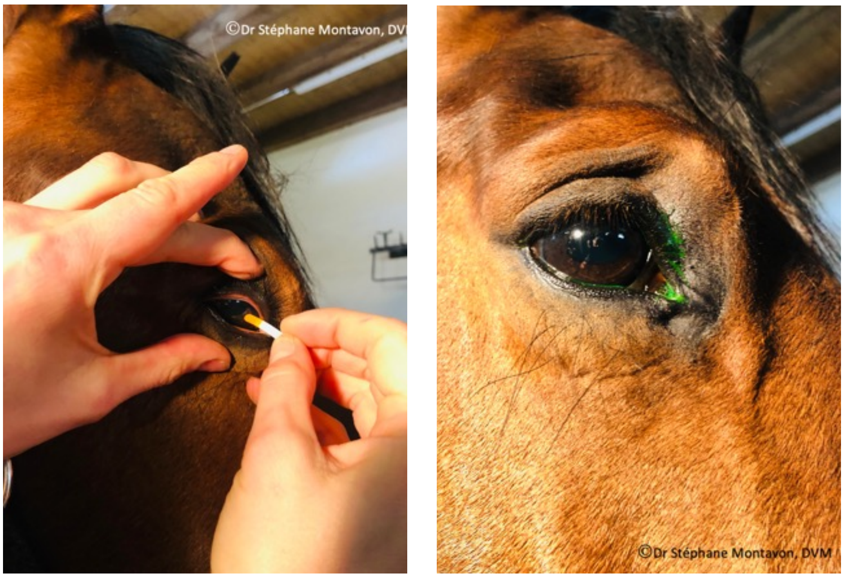

Figure 2: *Fluorescein strips are also used in horses to evaluate the quality of the corneal surface.* ***Source:*** *Dr Montavon*

binocular vision over an angle of approximately 60 to 80 degrees, meaning that they can see objects in front of them with both eyes at the same time despite a lateral position of the eyeballs. This allows them to judge distances and perceive depth. They have a wide field of vision, which allows them to see almost 360 degrees without moving their head. Their eyes are also very sensitive to movement in order to detect predators and other potential dangers. However, their perception of colour is not reduced compared to humans and they have difficulty distinguishing certain shades of red, green and blue.

Cones versus rods

The ability to perceive visual images depends on the amount of information available on the retina. There are two main categories of photoreceptors: rods and cones. Rods are responsible for vision in low light conditions (scotopic); cones are less sensitive to low light levels and are responsible for vision in brighter conditions (photopic). In the equine retina, rods outnumber cones by about 20 to 1 (3). A study of factors affecting the visibility of stimuli to horses found that bright daytime conditions were less favourable to the rod-dominated equine eye than lower light levels (4). Although bright (photopic) conditions optimise visual performance for humans, scotopic conditions are advantageous for the horse. Both categories of photoreceptors (rods and cones) synapse with bipolar cells, which in turn synapse with retinal ganglion cells. A relatively large number of rods (up to 45) synapse with each bipolar cell and provide poor spatial resolution compared to cones (5). Cones are less sensitive to low light levels but offer better spatial resolution due to their neural connections (in the human fovea, each cone is connected to a single bipolar cell). Cones also respond to light faster than rods, which improves temporal resolution (5).

Visual acuity (the ability to perceive detail) can be estimated by assessing the type of photoreceptors present in the retina, their connections with the bipolar cells, and the size and density (and hence receptive fields) of the retinal ganglion cells. The predominance of rods over cones in the equine retina is likely to limit their ability to perceive detail, particularly in comparison with human vision. It can therefore be concluded that equines are more sensitive to contrast than to colour

(2). A simulation of this difference was obtained with the Chromatic Vision Simulator software®. Figures 7 and 8 show the same photograph as seen by a human (Figure 7) and a horse (Figure 8). The differences are striking and allow a better understanding of the notions of trichromatic vision in humans versus dichromatic vision in horses.

Although the horse does not have an area of the retina consisting entirely of cones (as in the central area of the human fovea) (6), a higher percentage of photoreceptors has been found to be cones in the visual stria area (3, 7). In the visual stria area (which is located along a straight horizontal line dorsal to the optic disc), the density of retinal ganglion cells is higher than in other areas of the retina (8). The density was found to be higher at the temporal end of this visual line (8, 9, 10) which is the area responsible for binocular vision. The binocular portion of the visual field is located down the nose of the horse and is limited to between 60 (11) and 80 degrees (9). Harman et al., and Crispin et al. (9, 11) have also noted the existence of a blind spot in front of the forehead.

Ehrenhofer et al. (12), found that in most of the equine retina there are significant spaces between large ganglion cells that receive input from multiple amacrine cells. The rapid conduction of the axons of these large ganglion cells and their connections with the amacrine cells suggests that the horse is particularly sensitive to subtle changes in illumination and stimulus movement (12). The sensitivity of the retina to low levels of light is increased by the tapetum lucidum reflecting light through the photoreceptor layer (13) at the expense of resolution by scattering this light (8). In the horse, the lower edge of the tapetum coincides with the location of the visual stria (8), and it extends to form a rounded triangle in the upper half of the retina (13). The position of this reflective layer will increase the horse's sensitivity to light, particularly that reflected from the ground (14). These factors result in the horse's rapid response to sudden movement in the peripheral visual field, which, although a useful adaptation to escape predators, is often undesirable when working with horses and persists regardless of the level of training.

Consequences for equine learning

The characteristics of the equine eye reflect the requirements of the horse's natural lifestyle. Wild horses spend approximately 50–60% of their time grazing, with their heads down and their eyes close to the ground (15). They often live in open grasslands and are exposed to predation. Horses are cathemural and feed both during the day and at night, but their feeding behaviour is at its peak after

Figure 3: *Horses have a third eyelid in the nasal canthus of the orbital cavity. The role of this rare anatomical structure is to moisten the cornea when they are running and galloping at high speed.*
Source: *Dr Montavon*

Figure 4: *The shape of the pupil is oval and horizontally oriented. This shape allows horses to have almost complete vision while grazing with their heads close to the ground.* ***Source:*** *Dr Montavon*

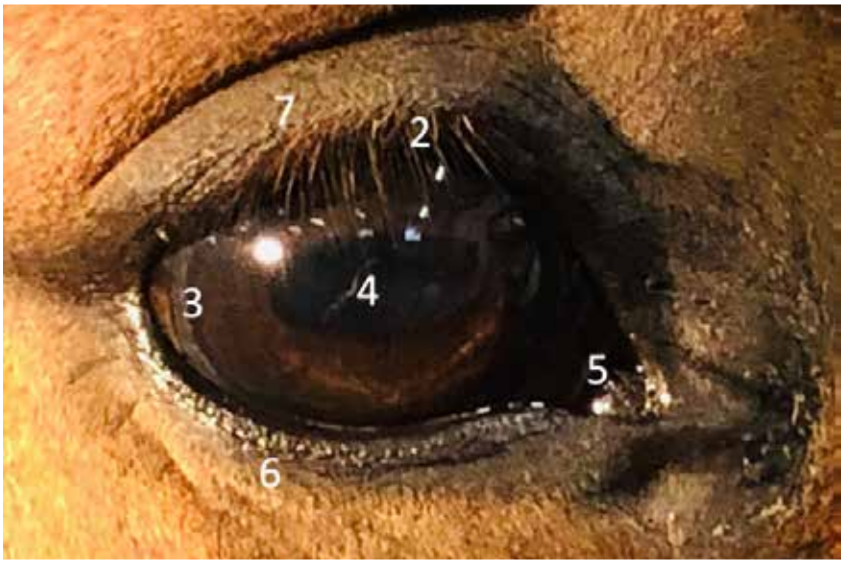

Figure 5: *External anatomical structures of the equine eye –*
2 = Eyebrows
3 = Iris
4 = Pupil
5 = Lacrimal duct
6= Lower eyelid
7 = Upper Eyelid
Source: *Dr. Montavon*

dawn and before dusk (15). When the horse lowers its head to graze and observe ground stimuli, the image is projected onto the most sensitive area of the retina. These adaptations of the equine visual system provide the horse with an effective early warning system to detect approaching predators. The lateral position of the equine eye provides a large visual field, most of which is monocular (9). The eye is adapted to function in low light conditions and has a rod-rich retina (3) and a reflective intraocular structure, the tapetum lucidum (13). Together with other visual characteristics, these adaptations have evolved to reduce the vulnerability of the horse in its natural environment. The impact of each of these features on the horse's ability to perform specific tasks needs to be considered both in the design of experimental learning studies and in the interpretation of the results.

Recent data on the structure and function of the equine eye can be used to explain the results of previous studies on the horse's ability to perform visual tasks. However, the behavioural study of equine vision and how it may affect the learning ability of the horse has so far been limited by two factors. First, without detailed evidence of retinal structure, the visual characteristics of the stimuli available to the horse and the factors that affect this visibility have necessarily been the result of conjecture (largely based on the characteristics of human visual perception). Second, other behavioural evidence of this visual ability has been, at least in part, limited by the time required to train the horse to make visual discriminations with the consistency required to draw conclusions about what it can actually see. Despite these limitations, behavioural evidence of the horse's ability to use pictorial cues to depth (16, 17), to use stereoscopic vision to judge depth and distance (ability to see depth based on binocular disparity (17, 18) and to see certain colours (18, 19, 20, 21) has been ascertained.

The importance of height in stimuli presentation

The link between the horse's learning ability and the characteristics of the equine visual system (described above) needs to be investigated in more detail. In their review, Murphy J. and Arkins S. (1) discuss the results of a first series of studies on equine visual discrimination (22, 23) in relation to the effect of age and sex in the horses tested. Stimulus position is another feature that has been shown to influence performance in these tasks. In the first study conducted (22), horses were trained to select a box of feed covered with a black cloth from two other boxes of ordinary feed. The black cloth was then repositioned above or below the box containing the food reward (23). Although more errors were made when the black cloth was placed in either of the new positions, performance was more accurate when the black cloth was placed in the lower position than when it was placed in the upper position. As mentioned above, when the horse lowers its head to observe stimuli on the ground, the image is projected onto the most sensitive area of the retina (9). When approaching an object with the head lowered, the binocular field is directed towards the ground and should allow the horse to see the stimuli. However, if the stimuli are presented at a higher level and the horse does not raise its head sufficiently, they may disappear from view if they are aligned with the horse's forehead. The position of the tapetum lucidum also accentuates the light reflected from the ground, making low level stimuli more noticeable to the horse than those at a higher level (14). The height at which visual stimuli are presented to the horse is therefore likely to affect its performance.

Visual discrimination training has been used to assess learning in horses, with stimuli usually presented at a height of 1 metre or more (24, 25). The initial conclusions from Gardner, P. (22, 23) that low level stimuli resulted in fewer errors than high level stimuli do not appear to have been taken into account. While placing stimuli at the "eye level" of human subjects is not generally debated, the "eye level" of the horse depends on the position of the head and neck. As Saslow, C.A. notes (4), the position of the head and therefore the level at which the eye is raised is important for projecting the image onto the most sensitive areas of the retina, especially when the horse is in motion. A more recent study has provided further evidence of the effect of stimulus height on visual discrimination in horses. When eight horses were trained to perform a simple two-choice black/white discrimination task with stimuli presented at one of two heights (ground level or 70 cm above ground level), performance was better when the stimuli were presented at ground level (26). In simple visual discrimination tasks, the increased sensitivity to ground-level stimuli, which is partly related to the reflective function of the tapetum lucidum, appears to be an advantage for the horse. However, in more complex discriminations, the associated lack of resolution may prove to be a disadvantage. For example, the shapes used as discriminative stimuli in the first study (24), and those used in the relational discrimination tests (25), may appear less clear to the horse if presented on the ground. Further studies are needed to determine whether the positional advantage would be lost in the discrimination of more complex stimuli or whether the increased attention that appears to be given to ground-level stimuli would still facilitate learning.

Visual acuity

In addition to the importance of presenting stimuli at an optimal height, when testing the horse's learning ability with visual stimuli it is important that these are of a size and distance that are clearly visible to the horse. Even in the area of visual striation, the horse has a limited ability to see detail compared to humans. Anatomical data have estimated the maximum visual acuity in the area of the visual line to be about 16.5 cycles/degree, with much lower acuity (3.3–3.5 cycles/degree) in other retinal areas (9). Behavioural evidence for visual acuity in horses has also been obtained. Using a two-choice visual discrimination task, Timney, B. et Keil, K. (16) assessed the ability of three horses to select a stimulus consisting of high-contrast gratings (vertical stripes that varied in spatial frequency) against a negative stimulus whose spatial frequency exceeded the animals' resolution

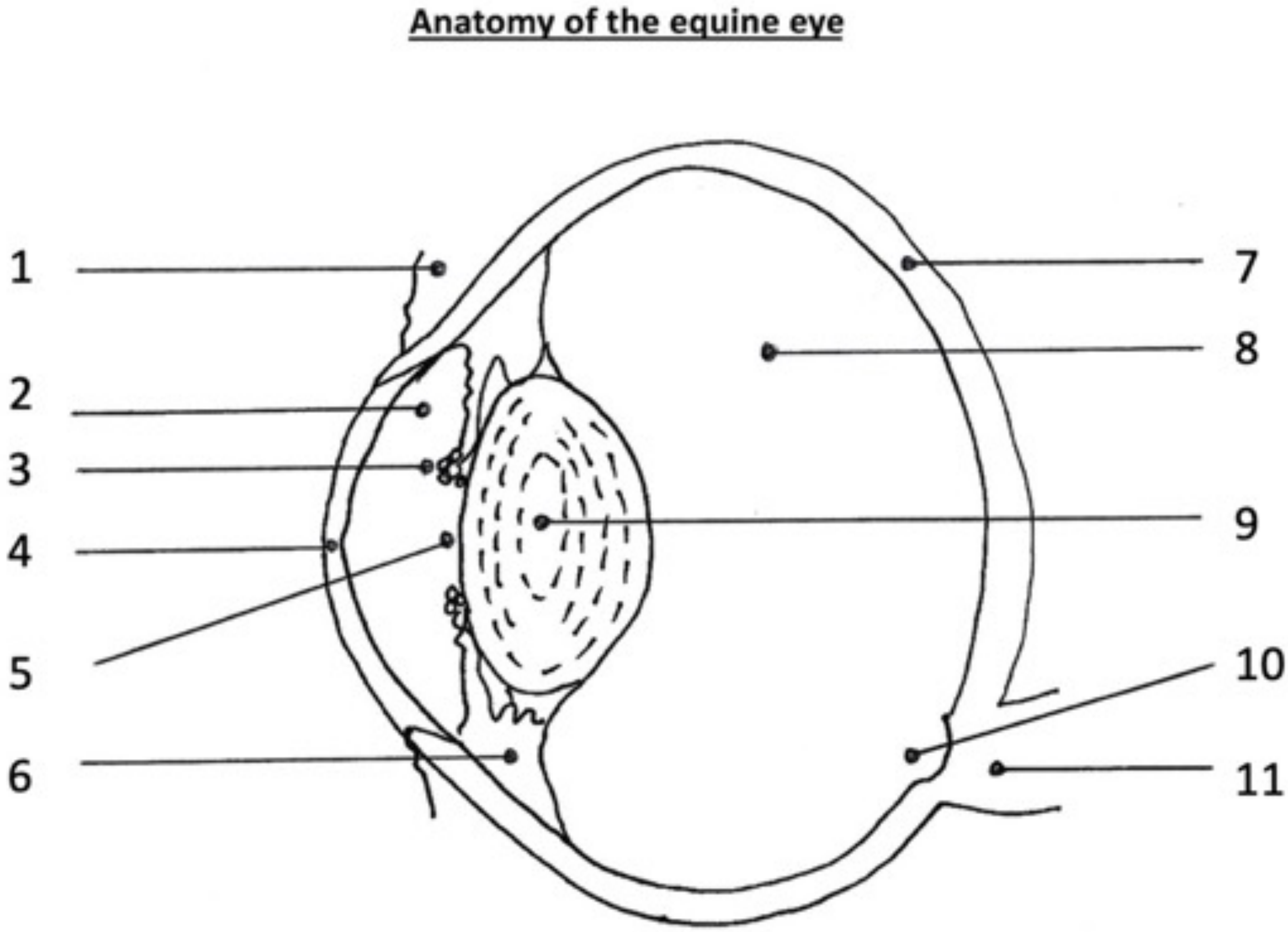

Figure 6: *Drawing of the internal anatomical structures of the equine eye – 1. Conjunctiva; 2. Aqueous chamber; 3. Corpora nigra; 4. Cornea; 5. Pupil; 6. Iris; 7. Retina; 8. Vitreous chamber; 9. Lens; 10. Optic disc; 11. Optic nerve.* ***Source:*** *Dr Montavon*

acuity. A range of values was obtained, the highest acuity being 23.3 cycles/degree and the lowest 10.9 cycles/degree. Individual variation in (horse) size and approach to the task was attributed to the cause of this variation. In comparison, although acuity varies in humans, the resolution limit of a normal observer is between 50 and 60 cycles/degree (27). This level of acuity is confined to the central region of the fovea, with values between 35 and 40 cycles/degree for most of the visual field (28). It is clear that across the entire visual field, the human observer can see much more detail than the horse. When assessing learning ability using visual tasks, care must therefore be taken to ensure that the stimuli presented are clearly visible to the horse and that performance deficits are not solely a consequence of perceptual constraints, unless visual ability is being investigated.

Colour vision and acuity

As in humans (29), visual acuity in horses varies according to the colour of the stimulus. Acuity with blue targets was found to be lower than with other colours, including yellow. While the horse could detect a five-millimetre-wide perpendicular yellow line at a distance of 3.3 metres (equivalent to 18.46 cycles/degree), a blue line had to be 20 millimetres wide to be detected at the same distance (equivalent to 2.9 cycles/degree) (19). These values correspond to the acuity values obtained for the visual stria and peripheral retina respectively (9). This is likely to be a result of the relative distribution of the two different types of cones, with short-wavelength photoreceptors being less prolific than medium-long wavelength photoreceptors in the visual stria (7). When visual stimuli are presented to the horse, in order to ensure that they are visible regardless of colour, they should be of such a size that when viewed at the assigned distance the visual angle is greater than 0.5 degrees.

The link between what is now known about the structure and function of the equine eye and the behavioural evidence of what horses can see is important. As well as providing an explanation for previous findings, it is now easier to make informed predictions about the visual abilities of equines, which can then be tested behaviourally. The correlation between visual mechanisms and behavioural performance was recently demonstrated in a study of colour vision in horses (30). Behavioural studies on the ability of animals to see colours have generally involved training them to distinguish between chromatic and achromatic stimuli, with all other cues (particularly differences in brightness, olfactory and spatial cues) being ignored. Four colours (red, green, blue and yellow) have been used previously to test the horse's ability to distinguish colours using this method. As noted by Murphy J. and Arkins S. (1), there have been conflicting reports on the colours that horses could distinguish from greys (19, 20, 21, 31). However, there is general consensus that equine eyes have two types of cones (and therefore photopigments) and are classified as dichromatic. The spectral peak values of these two photopigments have been estimated to be 429 nanometres (nm) and 545 nm (32). Using these values, it is possible to predict the effect that a colour (whose reflectance spectrum is known) will have on the photopigments of the horse's cones. The effectiveness of this method was confirmed when significant correlations were found between the ability of horses to discriminate fifteen different colours of various greys and the predictions made. Cone excitation ratios were calculated for each colour and then compared to the constant cone excitation ratio calculated for the achromatic stimuli (the greys). The extent to which the ratio for the colour differed from that for the greys was used to predict how colourful the stimulus appeared to the horse. The colours predicted to be the most colourful to the horse were also those that were most easily differentiated from grey. Another study showed that when horses were offered a choice between pairs of colours (selection of either colour resulted in a food reward), the colours predicted to be the most colourful were chosen most often (33). As in an earlier study from Grzimek B. (19), yellow was the most frequently chosen colour, followed by orange and then blue. It is clear that, at least with regard to colour, the visual characteristics that most attract the horse's attention can be predicted by analysing the characteristics of the equine visual system. The idea clearly expressed in the study of equine learning behaviour (1), that the learning ability of the horse is related to survival requirements in a specific ecological niche, also applies to their visual ability. Furthermore, the learning behaviour of equids, at least in visual tasks, depends on the characteristics of their visual system. The ability to focus on the ground when grazing while scanning the horizon for potential threats (9) is advantageous for predation avoidance, but may well limit the focal attention required by some tests of learning ability (34). The importance of recognising stimuli either as beneficial or a potential threat, without a second chance, may limit the horse's ability to reverse previously learned associations. Although the horse has been shown to readily reverse spatial cues, once visual cues are associated with a reward, it appears to be resistant to reversal (35). This has been cited previously as evidence of a lesser capacity for learning compared to other species (36). The horse has also been found to have difficulty applying responses learned in one task to a new task (37). It seems likely that the formation of specific associations and the lack of generalisation exhibited by the horse reflect strategies that have evolved to promote survival. As befits a herd-dwelling prey species, the horse's ability to respond to minimal visual cues given by conspecifics or human trainers is renowned. In the famous case of Clever Hans, the horse that apparently demonstrated his ability to count, the horse in question was responding to minimal changes in tension from his trainer. Unbeknownst to the trainer, Mr. von Osten, he changed his posture slightly once the horse had typed in the correct number (38). Further study of the horse's ability to respond to such small visual cues could contribute to the development of effective training methods and increase human awareness of unintentional cues. In line with previously cited Murphy J. and Arkins S. (1), the evidence presented here confirms that an understanding of visual perception is essential for the further study of equine learning. Furthermore, human visual perception should not be relied upon when designing visual tasks for the horse.

Conclusion: The characteristics of the equine visual system are well documented, but there is a need to further demonstrate the impact they have on learning behaviour (as well as on behaviour in general). Visual perception undoubtedly determines the ability to learn visual tasks. Given the emphasis on this sensory modality in most studies of equine learning, it is necessary to consider both the visual ability and behavioural tendencies of the horse in order to improve our understanding of learning behaviour in this species.

Figures 7 and 8: *The Chromatic Vision Simulator® software was used to show colour vision and colour vision deficiencies. This software makes and displays a simulated image from either an integrated camera or image file in real time. What the human sees (trichromatic) and what the horse sees (dichromatic) is different. – (Source: Dr Stéphane Montavon, DVM, Swiss Armed Forces - Chromatic Vision Simulator®)*

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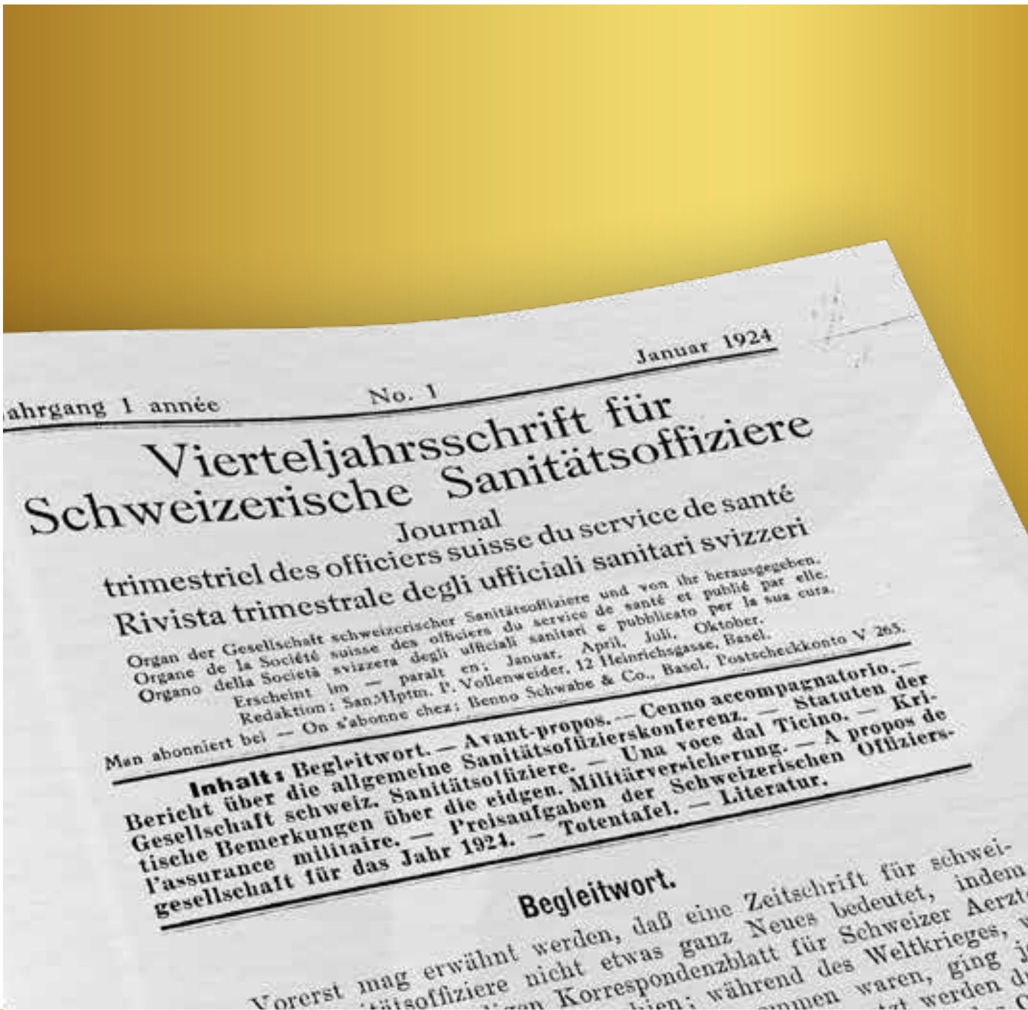
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