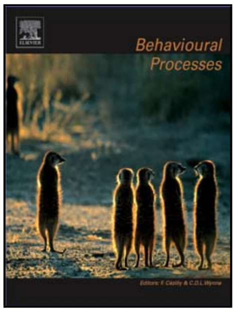
Accepted Manuscript



Title: The impact of visual perception on equine learning

Author: Carol Hall

PII: S0376-6357(07)00104-0
DOI: doi:10.1016/j.beproc.2006.09.017
Reference: BEPROC 1725

To appear in: *Behavioural Processes*

Received date: 7-8-2006
Accepted date: 12-9-2006

Please cite this article as: Hall, C., The impact of visual perception on equine learning, *Behavioural Processes* (2007), doi:10.1016/j.beproc.2006.09.017

Commentary

The impact of visual perception on equine learning

Carol Hall

School of Animal, Rural and Environmental Sciences, Nottingham Trent University,
Brackenhurst College Campus, Southwell,, Nottinghamshire NG25 0QF, United Kingdom

Address for correspondence:
School of Animal, Rural and Environmental Sciences
Nottingham Trent University
Brackenhurst College Campus
Southwell
Nottinghamshire, NG25 0QF
United Kingdom
carol.hall@ntu.ac.uk

Murphy and Arkins (2007) provide a comprehensive account of equine learning behaviour, evaluating evidence from a broad range of studies. Throughout their review they highlight the importance of identifying the natural abilities of the horse with the ultimate aim of optimising our training of this domestic species. It is clear that although the success of the horse-human relationship is largely dependent upon such training, our knowledge of the cognitive abilities of this species is sadly lacking. Given the role of the horse as an elite athlete and developments in other areas, for example in equine assisted therapy, an improved understanding of the factors that influence learning in this species is now required.

In particular, Murphy and Arkins (2007) identified two factors that are central to our understanding of the processes involved in equine learning. The first is the need for further investigation of the equine visual system and the effect that the features of this system has on both the acquisition of information from, and reaction to, the environment. The second is the identification of stimuli that are salient to the horse and thus attract the most attention. In order to optimise training, a primary requirement is that the animal is paying attention to relevant cues and ignoring irrelevant ones. By utilizing our knowledge of features of the equine visual system it is possible to present stimuli in a manner that is most likely to be noticed by the horse. The question of what attracts the horse's attention can thus be answered, at least in part, by a greater understanding of equine perceptual ability. In this commentary the link between the visual system of the horse and their ability to learn will be explored, in addition to related behavioural adaptations that may impact on their cognition.

Recent evidence relating to the structure and function of the equine eye can be used to explain the findings of previous studies into the ability of the horse to perform visual tasks. However, the behavioural investigation of equine vision and how it may affect the learning ability of the horse has until now been limited by two factors. Without detailed evidence of retinal structure, the visual features of stimuli that are available to the horse and factors that affect this visibility have necessarily been the result of guesswork (largely based on features of human visual perception). Further behavioural evidence of this visual ability has, at least in part, been restricted by the time it takes to train the horse to perform visual discriminations with the consistency required to draw conclusions about what they can actually see. Despite these problems, behavioural evidence of the ability of the horse to use pictorial depth cues (Timney and Keil, 1996), to use stereoscopic vision to judge depth and distance (the ability to see depth based on binocular disparity; Timney and Keil, 1999), and to see certain colours (Grzimek, 1952; Pick *et al.*, 1994; Macuda and Timney, 1999; Smith and Goldman, 1999) has been obtained.

Features of the equine eye reflect the requirements of the natural lifestyle of the horse. Feral horses spend approximately 50 – 60% of their time grazing with their heads lowered and their eyes near ground level (Mayes and Duncan, 1986). They often inhabit open grassland and are open to predation. Horses are active and feed during both the day and the night, but feeding behaviour peaks after dawn and before dusk (Mayes and Duncan, 1986). Adaptations of the equine visual system provide the horse with an effective early warning system for the detection of approaching predators. The lateral position of the equine eye provides an extensive visual field, the majority of which is monocular (Harman *et al.*, 1999). The eye is adapted to function in low light levels, possessing a rod-rich retina (Wouters and De Moor, 1979) and an intra-ocular reflective structure, the tapetum lucidum (Ollivier *et al.*, 2004). In conjunction with other visual features, these adaptations have evolved to reduce the vulnerability of the horse in its natural environment. The impact of each of these features on the ability of the horse to perform specific tasks should be considered in both the design of experimental studies of learning and in the interpretation of the results.

The ability to perceive visual images is dependent upon the amount of information available from the retina. Two main classes of photoreceptor are present, rods and cones. The rods are responsible for vision in low light (scotopic) conditions; the cones are less sensitive to low light levels and are responsible for vision in brighter (photopic) conditions. Within the equine retina the rods outnumber the cones by approximately 20:1 (Wouters and De Moor, 1979). In a study that investigated factors that affected stimulus visibility for horses it was found that bright daytime conditions were less favourable to the rod-dominated equine eye than lower light levels (Saslow, 1999). Although bright (photopic) conditions maximize human visual performance, scotopic conditions are advantageous to the horse.

Visual acuity (the ability to perceive detail) can be estimated by assessing the type of photoreceptors present in the retina, their connections with bipolar cells, as well as the size and density (and by implication, receptive fields) of the retinal ganglion cells. Both of the classes of photoreceptor (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 they provide poor spatial resolution compared to the cones (Barlow, 1988). 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 connects with a single bipolar cell). The cones also respond to light more quickly than the rods, hence resulting in improved temporal resolution (Barlow, 1988). The predominance of rods over cones in the equine retina is likely to limit their ability to perceive detail, particularly when compared with human vision. Although the horse does not have an area of the retina that consists entirely of cones (as in the central area of the human fovea; Curcio *et al.*, 1987), a higher percentage of the photoreceptors were found to be cones in the area of the visual streak (François *et al.*, 1980; Sandmann *et al.*, 1996).

Within the area of the visual streak (which is located along a straight horizontal line dorsal to the optic disc) retinal ganglion cell density was found to be higher than in other areas of the retina

(Hebel, 1976). The density was found to be greatest at the temporal end of this visual streak (Hebel, 1976; Harman *et al.*, 1999; Guo and Sugita, 2000), corresponding with 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 65° (Crispin *et al.*, 1990) and 80° (Harman *et al.*, 1999). Harman *et al.* (1999) also found that a blind spot existed in front of the forehead. When the horse lowers its head to observe stimuli on the ground, the image will be projected onto the most sensitive area of the retina. Ehrenhofer *et al.* (2002) found that in most parts of the equine retina there were large gaps between the ganglion cells, the majority of which were found to be large and to have input from many amacrine cells. The fast 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 motion (Ehrenhofer *et al.*, 2002). The resultant fast response of the horse to sudden movement in the peripheral visual field, although a useful adaptation to escape from predators, is one that is often unwelcome in ridden work and also one that persists regardless of the level of training.

Retinal sensitivity to low light levels is increased by the tapetum lucidum that reflects light back through the photoreceptor layer (Ollivier *et al.*, 2004) at the expense of resolution by the scattering of this light (Hebel, 1976). The lower margin of the tapetum in the horse coincides with the location of the visual streak (Hebel, 1976), and it extends to form a rounded triangle in the upper half of the retina (Ollivier *et al.*, 2004). The position of this reflective layer will increase the horse's sensitivity to light, particularly to that reflected from the ground (Saslow, 2002).

The link between the learning ability of the horse and features of the equine visual system (as detailed above) requires further investigation. In their review, Murphy and Arkins (2007) discuss the findings of an early series of studies into equine visual discrimination by Gardner (1937a and 1937b) in relation to the effect of age and sex of the horses tested. An additional feature that was found to affect performance in these tasks was that of stimulus position. In the first study carried out by Gardner (1937a), horses were trained to select a feed box covered with a black cloth from two other plain feed boxes. The black cloth was subsequently re-positioned to either above or below the box containing the food reward (Gardner, 1937b). Although more errors were made when the black cloth was placed in either of the new positions, performance was found to be more accurate when the black cloth was in the low position than in the high position. As stated above, Harman *et al.* (1999) found that when the horse lowers its head to observe stimuli on the ground, the image will be projected onto the most sensitive area of the retina. By approaching with the head lowered, the binocular field is directed towards the ground and should result in the stimuli remaining visible to the horse. In contrast, if stimuli are presented at a higher level and the horse fails to raise its head sufficiently it is possible that they will disappear from view if in line with the forehead of the horse.

The position of the tapetum also accentuates light that is reflected from the ground making low-level stimuli more noticeable to the horse than those at a higher level (Saslow, 2002). The height at which visual stimuli are presented to the horse is thus likely to affect performance.

Visual discrimination training has been used to assess learning in the horse with the stimuli generally being presented at a height of 1m or above (Sappington and Goldman, 1994; Flannery, 1997; Hanggi, 1999). The initial findings of Gardner (1937b), that stimuli placed at a low level resulted in fewer errors than those placed in a high position, appear to have been disregarded. While placing stimuli at “eye level” for human subjects is generally not a matter for debate, “eye level” for the horse is dependent upon head and neck position. As noted by Saslow (1999), the position of the head and consequently the level at which the eye is carried is important in projecting the image onto the most sensitive areas of the retina, particularly while the horse is in motion. Further evidence of the effect of stimulus height on visual discrimination in horses was found in a more recent study. When eight horses were trained to perform a simple two-choice, black/white discrimination with the stimuli presented at one of two heights (at ground level or at a height of 70 cm from the ground) performance was found to be better when the stimuli were presented on the ground (Hall *et al.*, 2003).

In simple visual discrimination tasks the increased sensitivity to ground level stimuli, which relates in part to the reflective function of the tapetum lucidum, appears to be advantageous to the horse. However, in more complex discriminations the associated lack of resolution may prove to be disadvantageous. For example, the shapes used as discriminative stimuli in the study by Sappington and Goldman (1994), and those used in the relational discrimination tests by Flannery (1997), may have appeared less clear to the horse if presented on the ground. Further study is required in order 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 paid to ground level stimuli would still facilitate learning.

In addition to the importance of presenting stimuli at an optimum height, when testing the learning ability of the horse using visual stimuli it is important that they are of a size that is clearly visible to the horse. Even in the area of the visual streak the horse has a limited ability to see detail in comparison with the human. 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 (Harman *et al*., 1999). Behavioural evidence of visual acuity in the horse has also been obtained. By using a two-choice visual discrimination task Timney and Keil (1992) assessed the ability of three horses to select a stimulus that consisted of high contrast gratings (vertical stripes whose spatial frequency was varied) against a negative stimulus whose spatial frequency was beyond the animals’ resolution acuity. A range of values was obtained, with the highest acuity being 23.3 cycles / degree and the lowest 10.9 cycles / degree. Individual variation in both the size (of the horse) and the approach to the task were attributed as the cause of this variation. In comparison, although acuity varies in the human, the limit of resolution of a normal observer lies between 50 and 60 cycles / degree (Woodhouse and Barlow, 1988). This level of acuity is confined to the central region of the fovea, with values of between 35 and 40 cycles / degree for the greater part of the visual field (Campbell and Green, 1965). It is clear that throughout the visual field the human observer can see in far more detail than the horse. Care must thus be taken when assessing learning ability using visual tasks that the stimuli being presented are clearly visible to the horse and that any deficits in performance are not purely the consequence of perceptual constraints, unless it is visual ability that is under investigation.

As in humans (Curcio *et al.*, 1991), visual acuity has been found to vary in the horse according to the colour of the stimulus. Acuity with blue targets has been found to be 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 (equivalent to 18.46 cycles / degree), a blue line had to be 20 millimetres wide for detection to be possible from the same distance (equivalent to 2.9 cycles / degree), (Grzimek, 1952). These values correspond with acuity values obtained for the visual streak and peripheral retina respectively (Harman *et al.*, 1999). It is likely that this is the result of the relative distribution of the two different cone types, the short wavelength photoreceptors being less prolific than the medium-long wavelength photoreceptors in the visual streak (Sandmann *et al.*, 1996). This may also result in blue being particularly visible in the peripheral visual field of both horse and human. When presenting visual stimuli to the horse, in order to guarantee visibility regardless of colour, they should be of a size that when viewed from the assigned distance, result in a visual angle that is greater than 0.5 degrees.

The link between what is now known about the structure and function of the equine eye and behavioural evidence of what horses can see is an important one. In addition to providing an explanation for previous findings, it is now more possible to make informed predictions about equine visual ability that can subsequently be tested behaviourally. The correlation between visual mechanisms and behavioural performance has recently been demonstrated in an investigation into colour vision in the horse (Hall *et al.*, in press). Behavioural studies into the ability of animals to see colours have generally involved training them to discriminate between chromatic and achromatic stimuli, where all other cues (in particular differences in lightness, olfactory and spatial cues) have been made irrelevant. Four colours (red, green, blue and yellow) had previously been used to test the ability of the horse to discriminate colours using this method. As noted by Murphy and Arkins (2007), there had been conflicting reports of which of these colours horses could successfully discriminate from greys (Grzimek, 1952; Pick *et al.*, 1994; Macuda and Timney, 1999; Smith and

Goldman, 1999). However, there was a general consensus that they possess two types of cone photopigment and are thus classed as dichromatic. Values for the spectral peaks of these two photopigments have been estimated at 429 nanometres (nm) and 545 nm (Macuda, 2000). By using these values it is possible to predict the effect that a colour (whose reflectance spectrum is known) will have on the cone photopigments of the horse. The effectiveness of this method was confirmed when significant correlations were found between the ability of horses to discriminate fifteen different colours from various greys and the predictions made (Hall *et al.*, in press). Cone excitation ratios were calculated for each colour 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. Those colours predicted to appear most colourful to the horse were also those that were most readily discriminated from grey (Hall *et al.*, in press). In a further study it was found that when the horses were offered a choice between pairs of colours (selection of either of the colours resulted in a food reward), those that were predicted to appear most “colourful” were selected most frequently (Hall *et al.*, 2005). As in an early study by Grzimek (1952), yellow was the colour selected most frequently, followed by orange then blue. It is clear that, at least in relation to colour, the visual features that attract the most attention from the horse can be predicted by analysis of features of the equine visual system.

The point so clearly made throughout the review of equine learning behaviour (Murphy and Arkins, 2007), that learning ability in the horse relates to survival requirements within a specific ecological niche, applies equally to their visual ability. It is also clear that equine learning behaviour, at least in visual tasks, is dependent upon the features of their visual system. The ability to focus on the ground when grazing while scanning the horizon for potential threats (Harman *et al.*, 1999) is advantageous for avoiding predation, but may well limit the focal attention required by some tests of equine learning ability (Lea and Kiley-Worthington, 1998). The importance of recognizing stimuli as either beneficial or a potential threat, with no second chances, may limit the capacity of the horse to reverse previously learned associations. While the horse has been shown to readily reverse spatial cues once visual cues are associated with a reward they seem to be resistant to reversal (Sappington *et al.*, 1997; Martin *et al.*, in press). This has previously been cited as evidence of a lesser ability to learn in comparison with other species. The horse has also been found to have difficulty in applying responses learned in one task to a novel task (McCall *et al.*, 2003). It seems likely that the formation of specific associations and the lack of generalization shown by the horse reflect the strategies that have evolved to enhance survival.

As also befits a herd dwelling prey species, the ability of the horse to respond to minimal visual cues given by either con-specifics or by human trainers is renowned. The famous case of Clever Hans, the horse that apparently demonstrated the ability to count, involved the horse in question responding to minimal changes in tension in his human trainer. Unbeknownst to him, the trainer, Mr von Osten, was thought to have changed his posture slightly once the horse had tapped out the correct number (Pfungst, 1965). Further investigation of the ability of the horse to respond to such minimal visual cues could aid in the development of effective training methods and increase human awareness of cues unintentionally given.

In accordance with Murphy and Arkins (2007) the evidence presented here confirms that an understanding of visual perception is central to further investigation of equine learning. Also, human visual perception should not be relied upon when designing visual tasks for the horse. Features of the equine visual system are well documented although further demonstrations of the impact that these have on learning behaviour (as well as on behaviour in general), is required. Visual perception undoubtedly determines the ability to learn visual tasks. With the emphasis that is put on this sensory modality in most studies of equine learning, consideration of both the visual ability and behavioural tendencies of the horse is necessary to improve our understanding of learning behaviour in this species.

Acknowledgements

The author would like to thank Helen Cassaday for her help and advice in the preparation of this manuscript.

References

Barlow, H.B. (1988) Physiology of the retina. *In:* H.B. Barlow and J.D. Mollon (Eds.) *The Senses.* 102-113. Cambridge University Press. Cambridge.

Campbell, F.W. and Green, D.G. (1965) Optical and retinal factors affecting visual resolution. *Journal of Physiology*. **181.** 576-593.

Crispin, S.M., Matthews, A.G. and Parker, J. (1990) The equine fundus 1: examination, embryology, structure and function. *Equine Veterinary Journal: Supplement* **10.** *(Equine Ophthalmology II).* 42-49.

Curcio, C.A., Sloan Jr., K.R., Packer, O., Hendrickson, A.E. and Kalina, R.E. (1987) Distribution of cones in human and monkey retina: Individual variability and radial asymmetry. *Science*. **236**. 579-582.

Curcio, C.A., Allen, K.A., Sloan, K.R., Lerea, C.L., Hurley, J.B., Klock, I.B. and Milam, A.H. (1991) Distribution and morphology of human cone photoreceptors stained with anti-blue opsin. *Journal of Comparative Neurology*. **312.** 610-624.

Ehrenhofer, M.C.A., Deeg, C.A., Reese, S., Liebich, H-G., Stangassinger, M. and Kaspers, B. (2002) Normal structure and age-related changes of the equine retina. *Veterinary Ophthalmology*. **5.** 39-47.

Flannery, B. (1997) Relational discrimination learning in horses. *Applied Animal Behaviour Science*. **54.** 267-280.

François, J., Wouters, L., Victoria-Troncoso, V., de Rouck, A. and van Gerven, A. (1980) Morphometric and electrophysiologic study of the photoreceptors in the horse. *Ophthalmologica*. **181.** 340-349.

Gardner, P. (1937a) The responses of horses in a discrimination problem. *Journal of Comparative Physiological Psychology*. **23.** 13-34.

Gardner, P. (1937b) Responses of horses to the same signal in different positions. *Journal of Comparative Physiological Psychology*. **23.** 305-332.

Grzimek, B. (1952) Versuche uber das Farbsehen von Pflanzenessern. *Zeitschrift fur Tierpsychologie*. **9**. 23-39.

Guo, X. and Sugita, S. (2000) Topography of ganglion cells in the retina of the horse. *Journal of Veterinary Medical Science*. **62.** 1145-1150.

Hall, C.A., Cassaday, H.J. and Derrington, A.M. (2003) The effect of stimulus height on visual discrimination in horses. *Journal of Animal Science.* **81.** 1715-1720.

Hall. C.A., Cassaday, H.J., Vincent, C.J. and Derrington, A.M. (2005) The selection of coloured stimuli by the horse. *BSAS Conference: Applying Equine Science, Research into Business.* (September 20-21). Royal Agricultural College. Cirencester. U.K.

Hall. C.A., Cassaday, H.J., Vincent, C.J. and Derrington, A.M. (in press) Cone excitation ratios correlate with color discrimination performance in the horse. *Journal of Comparative Psychology.*

Hanggi, E.B. (1999) Categorization learning in horses (Equus caballus). *Journal of Comparative Psychology.* **113.** 243-252.

Harman, A.M., Moore, S., Hoskins, R. and Keller, P. (1999) Horse vision and an explanation for the visual behaviour originally explained by the "ramp retina". *Equine Veterinary Journal.* **31.** 384-390.

Hebel, R. (1976) Distribution of retinal ganglion cells in five mammalian species (pig, sheep, ox, horse, dog). *Anatomy and Embryology.* **150.** 45-51.

Lea, S.E.G and Kiley-Worthington, M. (1996) Can animals think? *In:* Bruce, V. (Ed.) *Unsolved mysteries of the mind.* 211-244. Psychology Press Ltd. Hove, East Sussex.

Macuda, T. (2000) Equine colour vision. Ph.D Thesis. The University of Western Ontario.

Macuda, T. and Timney, B. (1999) Luminance and chromatic discrimination in the horse (Equus caballus). *Behavioural Processes*. **44**. 301-307.

Martin, T.I., Zentall, T.R. and Lawrence, L. (in press) Simple discrimination reversals in the domestic horse *(Equus caballus)*: Effect of discriminative stimulus modality on learning to learn. *Applied Animal Behaviour Science.*

Mayes, E. and Duncan, P. (1986) Temporal patterns of feeding behaviour in free-ranging horses. *Behaviour*. **96**. 105-129.

McCall, C.A., Salters, M.A., Johnson, K.B., Silverman, S.J., McElhenney, W.H. and Lishak, R.S. (2003) Equine utilization of a previously learned visual stimulus to solve a novel task. *Applied Animal Behaviour Science.* **82.** 163-172.

Ollivier, F.J., Samuelson, D.A., Brooks, D.E., Lewis, P.A., Kallberg, M.E. and Komáromy, A.M. (2004) Comparative morphology of the tapetum lucidum (among selected species). *Veterinary Ophthalmology.* **7**. 11-22.

Pfungst, O. (1965) *Clever Hans (the horse of Mr. Von Osten).* Edited by R.Rosenthal. Holt, Rinehart and Winston Inc. New York.

Pick, D.F., Lovell, G., Brown, S. and Dail, D. (1994) Equine color perception revisited. *Applied Animal Behaviour Science*. **42**. 61-65.

Sandmann, D., Boycott, B.B. and Peichl, L. (1996) Blue-cone horizontal cells in the retinae of horses and other Equidae. *The Journal of Neuroscience*. **16.** 3381-3396.

Sappington, B.F. and Goldman, L. (1994) Discrimination learning and concept formation in the Arabian horse. *Journal of Animal Science.* **72.** 3080-3087.

Sappington, B.K.F, McCall, C.A., Coleman, D.A., Kuhlers, D.L. and Lishak, R.S. (1997) A preliminary study of the relationship between discrimination reversal learning and performance tasks in yearling and 2-year-old horses. *Applied Animal Behaviour Science.* **53**. 157-166.

Saslow, C.A. (1999) Factors affecting stimulus visibility for horses. *Applied Animal Behaviour Science.* **61.** 273-284.

Saslow, C.A. (2002) Understanding the perceptual world of horses. *Applied Animal Behaviour Science.* **78.** 209-224.

Smith, S. and Goldman, L. (1999) Color discrimination in horses. *Applied Animal Behaviour Science*. **62**. 13-25.

Timney, B. and Keil, K. (1992) Visual acuity in the horse. *Vision Research.* **32.** 2289-2293.

Timney, B. and Keil, K. (1996) Horses are sensitive to pictorial depth cues. *Perception.* **25.** 1121-1128.

Timney, B. and Keil, K. (1999) Local and global stereopsis in the horse. *Vision Research.* **39**. 1861-1867.

Woodhouse, J.M. and Barlow, H.B. (1988) Spatial and temporal resolution and analysis. *In:* H.B. Barlow and J.D. Mollon (Editors) *The Senses.* Cambridge University Press. Cambridge. 133-164.

Wouters, L. and De Moor, A. (1979) Ultrastructure of the pigment epithelium and the photoreceptors in the retina of the horse. *American Journal of Veterinary Research.* **40**. 1066-1071.