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Commentary

The impact of visual perception on equine learning

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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.

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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,b) 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 1 m 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