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Commentary

Equine learning behaviour: accounting for ecological constraints and relationships with humans in experimental design

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Murphy and Arkins (2007) present a broad and interesting review which highlights our incomplete understanding of the idiosyncrasies of equine learning. Most studies of learning in horses have adapted general experimental paradigms to compare equine cognitive abilities with those of other species (McCall, 1990). As a result much of their review explores cross-species comparisons and previous attempts to place horses in a hierarchy of intelligence. Macphail (1996) argues that comparisons of performance on any given learning task are likely to be confounded by non-cognitive or 'contextual' species differences in motivation, attention and physical ability. Murphy and Arkins (2007) themselves describe how individual variation and poor correlation between performance on different tasks cast doubt on the appropriateness of this approach. They also highlight the impact of experimental design on test outcome, which is especially pertinent given the applied nature of much equine research. The ultimate objective of any experiment will influence its design and a number of the studies reviewed aimed to use learning tests to assess animals' suitability for training. Murphy and Arkins' (2007) goal is the application of learning research to maximise the potential benefits of the human–horse relationship to both parties. We would suggest that future studies could best achieve this by focusing on the development of unambiguous, horse-specific tests that combine rigorous scientific method with an appreciation of horses' evolutionary history, ecological niche and current management. Tailoring tests to species gives us greater confidence in their conclusions. Backed by biologically relevant experiments that robustly reflect equine cognitive and learning abilities, we are better placed to unravel the sources of variation both within and between species.

1. Ecological constraints and experimental design: the example of cue use

The cognitive capacities of a given species will be shaped by its environment and evolutionary history, and equine learning is best studied in this context (Nicol, 2005). An appreciation of how ecology and cognition interact helps us to understand differences in how species behave and learn (Healy and Braithwaite, 2000). Tests applied to horses have often been devised for substantially different species. Some negative or unexpected results probably stem from the application of methods which do not account for differences in equine sensory and neural capabilities or social and motivational factors. Consideration of ecological constraints can help generate predictions about a species' capacities, improve experimental design by clarifying what is being tested, and explain some intriguing phenomena observed in testing.

Murphy and Arkins (2007) mention that a species' behaviour will depend on how it experiences sensations, touching upon the evidence that horses attend to spatial cues more easily than visual ones in learning and reversing discriminations for food rewards (Fiske and Potter, 1979; Heird et al., 1986; Lansade et al., 2005; Sappington et al., 1997). This selective association between sensory stimulus and response is likely to reflect the biological relevance or reliability of different types of stimulus. Garcia and Koelling (1966) famously demonstrated that rats learn to associate subsequent illness with a novel flavour more readily than with a combined auditory and visual cue. Just as taste is more likely to be informative about the edibility of food than sound, integrating spatial information from various landmarks might be more reliable – for a grazing species navigating over long distances for food resources – than a visual snapshot of the food's location. Associating visual cues with a food reward might represent a rather artificial task that does not usefully reflect an individual's intelligence. Only very recently in domestication have visual signals such as the colour of a food bucket

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become salient regardless of their position. Nonetheless, visual cues would be useful in recognising visually distinct patches of preferred food plants such as clover whose locations vary over time. The apparent primacy of spatial cues is therefore an observation rather than an a priori assumption; separation of experimental confounds from cognitive constraints requires consideration of what constitutes an appropriate visual stimulus.

An appreciation of how evolutionary pressures shape a species' perceptual abilities can again be employed in designing appropriate discriminative stimuli and avoiding perceptual confounds. Remaining with the example of spatial and visual cue use, Martin et al. (2006) found that while horses could learn a spatial discrimination and six reversals within 300 trials, those using the visual cue of an overhead light failed to make even the initial discrimination. An examination of the literature suggests that the choice of stimulus may not have been appropriate to equine perceptive ability. Murphy and Arkins (2007) rightly suggest that further research into the equine visual system would be beneficial in linking perception to cognition and its applications in learning and training. They already highlight the equivocal results surrounding equine visual capacities such as the ability to distinguish green and yellow from grey (Macuda and Timney, 1999; Smith and Goldman, 1999). Equine visual acuity is similar to human peripheral vision with much of the visual system adapted to dim light and the perception of movement (Saslow, 2002). Horses demonstrate the almost all-round monocular vision typical of prey animals adapted to open habitat. The small area of binocular overlap is oriented down the nose (Harman et al., 1999) so that the head must be lifted look at distant objects. Combined with a horizontal 'visual streak' that appears to provide an area of improved acuity (Timney and Keil, 1992), this suggests that the position of a stimulus in the visual field can greatly affect a horse's ability to perceive it. Horses showed greater reactivity to floor colour than to identical mats positioned on the wall (Hall and Cassaday, 2006) and learnt a discrimination task more easily when stimuli were presented at ground level than at a height of 70 cm (Hall et al., 2003). The horse's sensitivity to movement and to ground level stimuli would be predicted by their importance in vital processes such as predator detection and food recognition, respectively.

If we are to make credible conclusions about the processes taking place in other species' brains, we must be very clear about what is being tested. Informed stimulus choice and presentation must be combined with awareness of what other information the experimental set-up provides. Nicol (2002) reviews a number of discrimination studies and describes various instances where the difficulty of spatial and visual tasks appears not be equivalent or where cue availability is confounded. To date, studies of equine cue use have all used stationary equipment that allows subjects to combine proximal and/or distal visual information with relational signals (e.g. left and right goals).

Murphy and Arkins (2007) also assert the importance of 'timing' (contiguity) in classical and operant conditioning, but most textbooks demonstrate that establishing an association between conditioned and unconditioned stimuli depends more on a strong *contingency* than on their temporal relationship (e.g. Hall, 1994). This applies equally to discrimination learning and the implications for experimental design merit further investigation; horses' apparent inability to learn a discrimination in a delayed response test (McLean, 2004) may actually reflect overshadowing or blocking by intervening events. Small movements, noises or even changes in light patterns that are imperceptible or constitute 'background noise' to experimenters may be sufficient to interfere with the formation of associations in species with different perceptual biases.

2. Domestication and the human–animal relationship: potential for developing new methods

Domestication is often viewed as a process in conflict with horses' natural behaviour. But by treating domestication as a recent episode in equine ecological history where certain traits have undergone intense selection, it can potentially be harnessed in experimental design to clarify the processes under test. Some people have suggested that domestication might reduce cognitive ability: the brain case volume of modern horses is 14% lower than that of much smaller wild Przewalksi's horse (Rohrs and Ebinger, 1993). However, particular capacities such as comprehension of human social signals are likely to have improved. Goodwin (2002) relates how wild horses routinely accept the presence of other social grazing species like zebra; such behaviour improves predator detection by effectively increasing group size. An existing inclination to attend to extra-specifics may have pre-disposed captive horses to respond to human-given cues; the domestication process will then have selected for the ability to comprehend human communicative gestures (Miklosi and Soproni, 2006).

Discussing the failure of a number of studies to demonstrate observational learning in horses, Murphy and Arkins (2007) propose using dominant demonstrators to resolve confounding social relations between observer and demonstrator. Yet dominant individuals may not always provide the most salient demonstrations. Capuchin monkeys learn most effectively from an experienced partner in a socially tolerant setting (Fragaszy and Visalberghi, 2004). Close proximity allows detailed observation of behaviour and so is predicted to facilitate the rapid acquisition of new skills or information. Where hierarchical relationships exist, affiliation and proximity vary across dyads and consequently affect individuals' chances of observing others (Coussi-Korbel and Fragaszy, 1995). If social rank influences opportunities (and so pre-disposition) to copy a dominant's behaviour, it will confound estimations of social learning ability. A practical alternative might be to capitalise on horses' learnt reliance on human cues. Most learning tasks are reinforced by food rewards, and horses are certainly accustomed to human actions signalling food provision. McKinley and Sambrook (2000) tested the ability of horses and dogs to use human-given cues in an object choice task, and found that two out of four horses tested were able to use touch and one dog could use pointing as a cue. In dogs, performance on a detour task could be improved by watching a human demonstrate the required route (Pongracz et al., 2001). Wolff and Hausberger (1996) drew on a human helper to demonstrate a detour and an instrumental task to 28 and 40 horses, respectively. Around half were