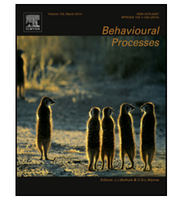
Behavioural Processes 126 (2016) 121–131

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Cognition and learning in horses (*Equus caballus*): What we know and why we should ask more

Lauren Brubaker*, Monique A.R. Udell

Oregon State University, Department of Animal & Rangeland Sciences, Corvallis, OR, USA

ARTICLE INFO

Article history:
Received 10 September 2015
Received in revised form 10 March 2016
Accepted 23 March 2016
Available online 24 March 2016

Keywords:
Horse behaviour
Horse welfare
Learning
Social cognition

ABSTRACT

Horses (*Equus caballus*) have a rich history in their relationship with humans. Across different cultures and eras they have been utilized for work, show, cultural rituals, consumption, therapy, and companionship and continue to serve in many of these roles today. As one of the most commonly trained domestic animals, understanding how horses learn and how their relationship with humans and other horses impacts their ability to learn has implications for horse welfare, training, husbandry and management. Given that unlike dogs and cats, domesticated horses have evolved from prey animals, the horse-human relationship poses interesting and unique scientific questions of theoretical value. There is still much to be learned about the cognition and behaviour of horses from a scientific perspective. This review explores current research within three related areas of horse cognition: human-horse interactions, social learning and independent learning in horses. Research on these topics is summarized and suggestions for future research are provided.

Contents

A horse that solves correctly problems in multiplication and division by means of tapping. Persons of unimpeachable honor, who in the master's absence have received responses, and assure us that in the process they have not made even the slightest sign. Thousands of spectators, horse-fanciers, trick-trainers of first rank, and not one of them during the course of many months' observations are able to discover any kind of regular signal

That was the riddle. And its solution was found in the unintentional minimal movements of the horse's questioner (Pfungst, 1911).

1. Introduction

On December 9th, 1904 a scientific report was published detailing how a horse, later known as 'Clever Hans,' fooled casual onlookers, horse experts, and scientists alike into believing that he could not only do complex mathematical problems, but tell time and demonstrate knowledge of pitch and music theory among other cognitive feats (Pfungst, 1911). Of course the horse was not aware of his trickery or of the mass media that propagated his fame. Instead Hans had learned to read human behaviour, specifi-

* Corresponding author at: Department of Animal and Rangeland Science, Oregon State University, Corvallis, OR 97330, USA.
E-mail address: lauren.brubaker@oregonstate.edu (L. Brubaker).

http://dx.doi.org/10.1016/j.beproc.2016.03.017
0376-6357/

cally subtle unintentional movements made by a questioner (most often a nodding of the head followed by a quick upward gaze at the horses face) that reliably signaled that the correct number of hoof stomps had been reached (Pfungst, 1911). Hans' genius was not illustrated by mathematical or musical ability but in his ability to carefully observe and learn about subtle human gestures that predicted what response would maximize his chances of obtaining a reward.

Horses are a common domestic animal often used for sport, companionship, and in a variety of working roles (*Equus caballus*). Domestic horses fill a unique niche in human cultures, as nearly all of them will undergo some type of extensive training during their lifetime (Hausberger et al., 2008). Given the diversity in human lifestyles, it comes as no surprise that there are a wide variety of beliefs on how horses should be trained, what they are capable of understanding, and how various training methodologies affect their welfare and relationship with humans. It is surprising, then, that comparatively little research has been done on the cognitive abilities of the horse, with nearly seven times less research done on horse cognition than on rat cognition (Cooper, 2007). The research that is available suggests that horses perform very successfully on a range of cognitive tasks including discriminative learning, memorization, and concept formation (Thomas, 1986; Murphy and Arkins, 2007; Hanggi and Ingersoll, 2009). As seen in the case of Clever Hans, horses demonstrate acute sensitivity to the actions and behaviours of other individuals, including humans (Pfungst, 1911; Hausberger et al., 2008; Lansade and Bouissou, 2008; Birke et al., 2011; Dorey et al., 2014); yet many areas of horse cognition and learning remain unexplored (Cooper, 2007; Goodwin, 2007; Murphy and Arkins, 2007).

Modern domesticated horses live in conditions that are in stark contrast to their wild ancestors and are often subject to training and management techniques that are contrary to their species-typical biological drives (Goodwin, 2007; Heitor and Vicente, 2007; McGreevy and McLean, 2007). This includes asking the horse to ignore their natural tendency to flee from situations that may be fearful for them (i.e., working with horses in novel and stressful environments such as carriage work or veterinary hospitals), and to both communicate and cooperate with another species that might otherwise be categorized as a predator: humans. Many horses, such as the racehorse, undergo a variety of management and training experiences. This often involves retraining and relearning throughout the lifetime of the horse (Goodwin et al., 2009). The exact implications of this for learning, cognitive performance and welfare are not well understood (Hausberger et al., 2008; McGreevy et al., 2009). Scientific knowledge of horses' perceptual world and cognitive abilities could aid in the design and implementation of training programs, as well as care and management systems, increasing the overall welfare of this species (Heitor and Vicente, 2007; Goodwin et al., 2009).

Like all animal cognition research, horse cognition can be tackled from a variety of angles using a variety of methods. Horses raised for different purposes, such as a horse used in hippotherapy versus a stock horse, may be exposed to different lifetime factors that could influence their behaviour and cognition in important ways. This, as Goodwin (2007) suggests, may lead to some discrepancies in the literature and can make seamless integration of scientific information available about the 'horse' as a species a difficult task. As a result, a larger body of research on horse behaviour and cognition than currently exists is needed to establish the full range of cognitive abilities and capacities of horses, and to better understand the interplay between genetics, environment and lifetime experiences that inform the behaviour of distinct populations and individuals. This review explores the current state of three related areas of horse cognition that are of central relevance to those working with horses in both scientific and applied contexts: human-horse interactions, social learning and basic discriminative learning by horses. Scientific challenges, welfare and management considerations are discussed.

2. Horse-Human interactions

Given the diversity of roles horses play in society, the horse-human relationship is an important area of study from both a basic and applied perspective (Hausberger et al., 2008). Horses and humans are often closely bonded, even to the point of some humans describing their relationship with their horse as being synchronous with them, particularly in the context of riding (Birke, 2007; Maurstad et al., 2013; Smith et al., 2016). Research has backed this claim up to some extent by showing that a horse's heart rate will increase in response to a rider's increased heart rate, regardless of outside stimuli (Merkies et al., 2014). Understanding the human-horse bond is imperative to the safety of horses and humans (Hawson et al., 2010; Thompson et al., 2015). This may be especially true in riding, therapeutic, and other working contexts. The relationship between humans and horses appears to be complex and dependent on a variety of factors, including the level of attachment humans feel towards their horse (DeAraugo et al., 2014), the emotional state of the human (Keeling et al., 2009), and the horse's past experience with humans (Sankey et al., 2010c).

In some cases horses have been shown to display acute sensitivity to and memory for humans and human actions. Research suggests that horses can recognize and remember individual handlers and trainers and whether past interactions with those individuals had been positive or negative (Sankey et al., 2010b; Stone, 2010; Lampe and Andre, 2012). Horses can distinguish human faces and voices and can match familiar voices to familiar faces (Proops and McComb, 2012). Horses appear to use multisensory information, including visual, olfactory, and auditory signals to distinguish between humans, as well as to assess human attentional state. One study found that when these signals were mixed (when one person came into the visual field of the horse while an audio recording from another person was played) the horses looked in the direction of the signals quicker, more often, and for longer (Lampe and Andre, 2012). In a different study, horses were more obedient if a familiar person was looking at them (rather than inattentive) when they gave a verbal command; horses monitored an unfamiliar person more often and for longer periods of time compared to a familiar person (Sankey et al., 2011).

Research has shown that operant conditioning can be used to teach horses to distinguish pictures of human faces with high precision, even when presented with identical twins (Stone, 2010). Stone (2010) demonstrated that privately owned horses react differently in the presence of unfamiliar people in their territory. When each horse was given a choice to occupy the presence of the familiar person, the unfamiliar person, or an empty space, horses spent more time on the side of the pen with the familiar person or in the empty space than with the unfamiliar person (Stone, 2010). Horses appear to distinguish between attentive and inattentive humans with access to food rewards, preferring to approach humans who are facing and looking at them to those who are not (Proops and McComb, 2010); similar results have been found by Krueger et al. (2010). Research has indicated that a horse's attentional state is important to a horse's ability to learn a verbal command and that a horse's attention can be manipulated based on the type of reward offered to the horse during training (Rochais et al., 2014). Lesimple et al. (2012) showed that horses that failed to complete a task demonstrated by an experimenter (opening a chest for a food reward) spent more time showing exploratory behaviours towards the experimenter and investigating the chest but not attempting to open it. Similar to findings with dogs (Topál et al., 1997), the authors suggest that the horses were attending to the human more often due to an expectation that the human would provide the food for them, but they acknowledge that more research is needed to better understand this finding (Lesimple et al., 2012). This suggests that horses are likely sensitive to interpersonal contexts that have led to positive outcomes in the past, and may be strong candidates for additional research on individual recognition and theory of mind and sensitivity to attentional state.

Another area that has received some attention is the ability of humans to communicate with horses using gestures (i.e. pointing), modeled after research conducted originally with chimpanzees but, more recently, used to assess the social cognition of a wide range of species including dogs and cats (Udell et al., 2010). Maros et al. (2008a) tested the ability of twenty horses to locate apple pieces in one of two buckets – with the "correct" bucket being the one that the experimenter pointed to. Four different pointing methods were used: distal dynamic-sustained (the experimenter's pointing hand was at least 80 cm from the bucket and they kept their hand in the pointing position while the horse made a choice), distal dynamic-momentary (the experimenter lowered their hand so that it was not raised while the horse was making a choice), proximal momentary pointing (the experimenter's pointing hand was ten centimeters from the bucket), and proximal dynamic-sustained pointing with gazing. Horses excelled at all of the pointing tasks except for the distal dynamic-momentary pointing. This is reflective of findings in other animals, as it is thought that distal dynamic-momentary pointing is much more cognitively demanding than other pointing styles (Maros et al., 2008a).

Some have suggested that horses may rely on stimulus or local enhancement in human-guided choice tasks, instead of a referential understanding of the gestures themselves (Krueger et al., 2010; Proops et al., 2010; Lovrovich et al., 2015). More research in this area is required to tease apart these possible mechanisms. Given that some companion animals, including dogs, have performed successfully using momentary distal points (Udell et al., 2010), these findings have raised comparative questions about the social cognition of horses versus other domesticated species (McKinley and Sambrook, 2000), as well as questions about lifetime factors that could contribute to the development of human-gesture responsiveness by horses.

This is evident in a recent study that asked if horses with different training backgrounds varied in their ability to utilize human pointing gestures to locate hidden food. Dorey et al. (2014) compared ten horses originally trained using "traditional" training methods with ten horses originally trained using natural horsemanship methods. Natural horsemanship training often claims to employ a greater use of human gestures as discriminative stimuli than traditional training, with trainers instructing the horse visually from the ground (Parelli et al., 1993). To assess the effects of these different training histories on gesture responsiveness, researchers used a momentary distal point to indicate which of the two buckets (placed one meter from the experimenter) was "correct". Similar to Maros et al. (2008a), researchers found that neither of the two groups initially performed above chance on this task. When given an additional sixty trials (where correct choices were always positively reinforced in the same way – the horse was allowed to eat the preferred food item), the horses in the natural horsemanship group were able to learn to follow the cue with significantly greater success than those in the traditional group (Dorey et al., 2014). Past training style appears to influence horses' success in human-guided tasks and may influence other areas of cognitive ability (Dorey et al., 2014). This finding is supported by Proops et al. (2013) who found that horses seem to develop the skill of following human gestures as they age and that lifetime experience plays an important role in this development.

3. Social and observational learning

Horses are herd animals, thought anecdotally to be capable of learning and copying behaviour from conspecifics (Lindberg et al., 1999; Krueger and Flauger, 2007; Ninomiya, 2007). A common training method that is typically utilized by horse trainers is one in which human handlers employ observational learning methodology to train younger horses by using older, well-trained horses (Murphy and Arkins, 2007). This practice is heavily utilized in horse training and has important implications for welfare of the horse, particularly as it relates to group housing and the changing environment and management that horses often undergo (Nicol, 2002; Christensen et al., 2006). Despite this, few studies have been completed to better understand how effectively horses learn from conspecifics (Murphy and Arkins, 2007). In the scientific literature, observational learning is defined as learning in which a bystander acquires a new skill or behaviour by watching the actions (and the consequences) of another individual, usually a conspecific (Zentall, 1996). Observational learning has been demonstrated in many species (Zentall, 1996). Evidence of observational learning in horses has been varied, despite anecdotal claims (Baer et al., 1983; Baker and Crawford, 1986; Clarke et al., 1996).

Some studies have suggested that horses only learn from conspecifics when demonstrators are familiar and dominant to them within a herd setting. In one such study observer horses had the opportunity to watch a familiar dominant, familiar subordinate, or unfamiliar individual learn to follow a trainer around a pen (Krueger and Heinze, 2008). The researchers found that subordinate horses mimicked the behaviour of the dominant, familiar horses, even in cases where the dominant horse engaged in the incorrect response (failed to follow the trainer around the pen). Dominant horses did not learn from subordinate conspecifics, nor did horses learn from unknown conspecifics (Krueger and Heinze, 2008). In support of this, Andrieu et al. (2015) found that horses that are "lower ranking" in a herd setting are followed to a hidden food source less often than higher-ranking horses (Andrieu et al., 2015).

Clarke et al. (1996) showed that horses failed to follow pattern cues (i.e., using a black and white pattern as a visual cue over a solid yellow colour) when observing a horse performing a simple discriminative task but did show a slight tendency to follow spatial cues (decreased latency to approach the location of the food reward) after such an observation. This may be related to the fact that horses seem to excel at spatial learning over pattern-based learning more generally, making it an easier task (Hothersall et al., 2010). Other research has shown that horses do not perform better in spatial detour tasks (a maze) after given the opportunity to watch a demonstrator being led down the correct route three times (Rørvang et al., 2015).

Lindberg et al. (1999) failed to find evidence of social learning when observers watched a demonstrator (trained to open a bin with a food reward inside by pressing on a pedal) before encountering the task themselves. Other factors appeared to influence task performance. Younger horses showed more investigative behaviour and interacted with the testing apparatus more than older horses. While they were not more successful on this particular task, increased exploration in the presence of novel stimuli could give younger horses an advantage in other learning contexts (Lindberg et al., 1999). Other research has supported this finding by demonstrating that horses fail to learn an instrumental task (opening a container by sliding a lid with their muzzle) after viewing an observer performing the task successfully but do interact with the apparatus more after viewing a demonstrator horse performing the task (Ahrendt et al., 2012). Breeds categorized as "non-warmblood" (a temperament classification given to categories of horses that are more calm, agreeable, and are generally stockier, as in ponies or heavy breeds such as draft horses) individually learned the basic operant task faster than warmblood breeds (a temperament classification given to categories of horses that are more excitable and energetic; horses such as thoroughbreds and Arabians) (Lindberg et al., 1999). This finding has been expanded on by Krueger et al. (2014), who found that younger, lower-ranking, and more exploratory horses were able to learn to pull a rope and open a drawer containing food after observing an older herd member perform the task. The younger observers learned faster and completed more experimental trials than older observers; whether this is due to the horse's age, rank, increased exploratory tendencies or all of the above is less understood (Krueger et al., 2014).

Inconsistent evidence of social learning in horses to date may have more to do with study design, coupled with a shortage of research on this question, rather than the absence of observational learning skills on the part of the horse (Murphy and Arkins, 2007). Many past studies have failed to control for the prior experiences of the horses, or the relationship between the observer and the demonstrator, making it difficult to draw strong conclusions (Krueger and Flauger, 2007). Given the discrepancies between these seemingly negative results and anecdotal claims of social learning in the horse, more research in this area is needed; either to determine the contexts under which social learning is more likely to occur, or to better understand the alternative processes at play – especially those that may look like social or observational learning to trainers.

4. Independent learning

4.1. Discriminative and generalized learning

The study of discriminative learning in animals not only provides insight about the basic individual learning capabilities of a species but can be used as a tool to learn about other areas of that species' cognition, including memory and perception as well as more complex problem solving and reasoning. This knowledge is important for understanding horse behaviour and cognition from a scientific perspective and may serve as a useful tool in training and management contexts. While research on discriminative learning in horses is still limited compared to many other species, a much longer history of research exists in this area. As with other areas of horse cognition, mixed results suggest more research is needed with careful attention paid to context, methodology and demographic factors that could influence performance.

Dating back almost a century, early studies suggested that horses could discriminate between three basic boxes when the boxes were placed at various heights and positions (left, middle, or right) by using a black cloth – the discriminative stimulus – to cover the correct box. Some of these horses were retested more than two years later and could still successfully discriminate between boxes using the same cue, despite no training between tests (Gardner, 1933). Since then researchers have attempted to better understand the parameters of this ability. In some cases, horses have been taught to lever press for a food reward, much like laboratory pigeons or rats, later using this behaviour to make choices in tasks requiring them to discriminate between a variety of stimuli (McCall et al., 2003), including complex patterns of shapes and colours to a degree that may suggest concept formation (Sappington and Goldman, 1994). Blackmore et al. (2008) demonstrated that horses could learn to discriminate between different hues of colour, although this ability was limited given that horses are dichromatic. Horses were less able to distinguish red and green from shades of grey compared to their ability to distinguish yellow and blue hues (Blackmore et al., 2008).

Horses show the ability to discriminate between 2D and 3D objects and generalize this ability when the objects are rotated in novel ways (Hanggi, 2010a). Interestingly, horses are more successful when viewing an object from the top and less successful when the object is viewed from the bottom. The researchers suggested that this difference may be due to visual cues (which are more easily seen from the top of 3D objects) or due to the fact that the horses are less familiar with viewing the bottom of objects in their day to day experience (Hanggi, 2010a). The knowledge that horses learn about and respond differently to objects based on orientation, colour, size and shape could be valuable in applied and training contexts, as it suggests that trained responses to certain props or environmental features may not automatically generalize to other similar items or features in the horse's environment. It suggests that scientific studies need to carefully control for these features when designing protocols for cognitive research in horses.

Horses have proved successful on at least some quantity discrimination tasks. When given a choice between two apples and one large apple of relatively the same volume, horses will choose two apples (Uller and Lewis, 2009). Researchers suggest that, similar to non-human primates and infants, horses could be attending to an object's surface area over the object's volume – objects that take up a greater surface area may be more "valuable" or appealing to the horse (Uller and Lewis, 2009). Whishaw et al. (2009) tested horses on their ability to remember where a pole on the ground was relative to their foot position, and results suggested that horses have excellent place-object memory (Uller and Lewis, 2009; Whishaw et al., 2009).

Horses appear capable of retaining learned information for extended periods of time. Hanggi and Ingersoll (2009) showed that horses could discriminate between previously trained rewarding and non-rewarding stimuli, such as 3D household objects and 2D photographs of those objects, for more than seven years after the initial training. Horses who had learned to categorized shapes with and without holes in the center and, in a second experiment, according to relative size (big or small) could correctly sort shapes and sizes nearly a decade after initial training, and could generalize these concepts to novel shapes with no additional training (Hanggi and Ingersoll, 2009). Horses have been shown to remember people (particularly trainers who use positive reinforcement) and conspecifics for up to eight months (with the potential for lasting up to 10 years), even after contact with the individual had ceased (Miller, 1995; Hanggi and Ingersoll, 2009; Sankey et al., 2010c)

Horses can learn to generalize across at least some visual stimuli. Gabor and Gerken (2012) found that Shetland ponies successfully generalized from geometric shapes to symbols (such as a peace sign or a musical symbol) presented on a computer screen in a matching to sample task within a maximum of eight testing sessions, with two ponies achieving learning criteria within the first session. Gabor and Gerken (2012) acknowledged that there was some difficulty in interpreting what the ponies learned over the course of the study and whether they had truly performed a matching to sample generalization, and suggest that it's possible the ponies used a procedural learning mechanism rather than learning concepts. Flannery (1997) found that horses could generalize across different shapes and letters with shared features in matching trials, and that this ability improved with additional training and reinforcement. When matching stimuli were placed farther apart or when the background stimulus was changed from the initial experimental conditions (from an uneven wooden surface with beams to a flat gray panel), horses could generalize information to these novel environments and presentations (Flannery, 1997).

Dougherty and Lewis (1991), asked horses to discriminate between a black circle 2.5 in. in diameter (the positive or rewarded stimulus) and a black circle 1.5 in. in diameter (the negative stimulus). Interestingly, when horses were presented with intermediate stimuli Dougherty and Lewis (1991) found that, unlike pigeons and humans, horses showed symmetrical generalization gradients (they chose stimuli that were closest in size to the originally rewarding stimulus on average), as opposed to asymmetrical generalization (where there is a tendency to choose exaggerated versions of the initially rewarded stimulus, i.e. choosing circles larger than the original positive stimulus on average, representing an avoidance of the negative stimulus). This may suggest that horses find negative stimuli, or the absence of reward associated with their selection, to be less aversive than most humans do. This hints at a fundamental difference between horses and other species, despite their ability to learn the basic task at the same rate, and could have a significant impact on how horses learn and respond to choice tasks in a variety of settings. Consequently, this may be an especially interesting area for future research.

Despite these intriguing findings, research suggests that there may be important limits to a horse's discriminative learning ability. For instance, while horses appear to discriminate between visual stimuli in novel tasks for a food reward, they may fail to use the same visual stimuli to solve new problems. McCall et al. (2003) used a striped board to signal a correct lever that a horse could press for a food reward. That same board was then used as a stimulus that could direct the horse left or right through a simple Y-maze toward a food reward. Horses were unable to navigate the maze correctly despite having used the signal succesfully in the lever-pressing context. McCall et al. (2003) suggested that their protocol may have been too lenient in the initial training of the visual stimuli, and that more training may have helped the horses generalize the use of this discriminative stimulus to novel contexts. These findings may alternatively suggest that horses are unable to generalize the use of discriminative stimuli to new situations or contexts. Horses may benefit from having distinct stimuli for different tasks, such as using one stimulus for spatial tasks and another for discrimination tasks (McCall et al., 2003).

While research would suggest that many horses can be successful on a wide range of discrimination tasks, variability in performance has made it difficult to draw conclusions about the species as a whole or applicability to horses kept in different settings (Dougherty and Lewis, 1991; Sappington and Goldman, 1994; Flannery, 1997). Breed, background, study design (especially the type of stimuli used), and a number of other factors appear to impact a horse's ability to succeed on discriminative learning tasks (Lindberg et al., 1999; Murphy et al., 2004; Murphy and Arkins, 2007; Sankey et al., 2010c; Henselek et al., 2012; Starling et al., 2013).

4.2. Reversal learning

Some research has suggested that horses may lack the ability to engage in reversal learning. While researchers have found that horses can be trained fairly easily in a basic discriminative learning task, such as discriminating between a black and white coloured food bucket for a reward, they appear to have difficulty "unlearning" that same task in a reversal protocol (Sappington et al., 1997), i.e. learning to go to the white food bucket that previously did not result in a reward. Some have suggested that the primacy effect (what was learned first is most salient in an individual's memory) may be crucial to a horse's ability to perform on certain tasks and may be difficult to overcome; therefore, reversal trials may not be an ideal measure of equine cognitive ability (Sappington et al., 1997; Innes and McBride, 2008; Sankey et al., 2010c).

Reversal learning does appear to occur under some conditions. When presented with varying stimuli that contrasted in both brightness and relative position, Fiske and Potter (1979) found that horses could successfully learn reversals after 20 trials. Horses that were faster at learning the reversal were rated as more trainable by an independent trainer (Fiske and Potter, 1979). To determine if the horses were using spatial cues or brightness cues to complete the reversal task, Martin et al. (2006) compared horses in a "visual" reversal learning condition to horses in a "spatial" reversal learning condition and found that horses in the spatial group made fewer and fewer errors over the course of six trials. Horses in the visual group struggled to even learn the initial discrimination task and were not subject to any reversal trials (Martin et al., 2006). Other studies have suggested that horses struggle with both basic discrimination and reversal learning based on visual characteristics of stimuli compared to spatial stimuli – although horses can often learn to discriminate visual cues with additional training (Hothersall et al., 2010). Horses may form learning sets, or "learn to learn," as subjects tend to commit less errors on each reversal trial as the experiments progress (Martin et al., 2006).

5. Applied considerations

5.1. The relationship between horse cognition, training and welfare

In addition to the pure scientific value of understanding horse behaviour and cognition, there are many practical applications for additional research in this domain. Greater knowledge about the behavioural and cognitive potential of domestic horses could shed light on the welfare status and needs of horses kept in a variety of captive settings. Likewise, understanding how a horse's genetics, welfare, environment and experiences work together to predict performance on cognitive tasks or training potential would be informative to scientists and horse handlers alike. In other words, integration of knowledge about horse cognition, biology and modern horse care/welfare practices will likely be of critical importance to a fully developed understanding of this species and the applications that could extend from this work.

Rivera et al. (2002) found no physiological differences (i.e. no differences in cortisol levels) between pastured versus stalled horses during basic training, including initial round pen work, desensitization to equipment (lead ropes, bridles, saddles, and saddle pads), and riding (walk, trot, and canter). Horses that were kept on pasture with other horses had lower overall training times, displayed less undesirable behaviours and required less desensitization time to novel equipment during training trials (Rivera et al., 2002). Søndergaard and Ladewig (2004) found that horses kept in group housing displayed less aggressive behaviours (such as biting and kicking) and passed a series of 43 training stages (including catching, tying, verbal commands for stop, walk, and trot, and free-jumping) faster than horses who were housed singularly (Søndergaard and Ladewig, 2004). Other research indicated that yearlings that were separated from conspecifics habituated to a novel stimulus and learned an instrumental task faster than yearlings kept in a group, suggesting that social separation may result in decreased emotional reactivity which increased the yearlings' learning ability (Lansade et al., 2012). This adds to a growing body of research which demonstrates that the horse's psychological state is important in learning, performance, and its relationship with humans (McBride and Mills, 2012; Starling et al., 2013; Merkies et al., 2014). The fact that living and testing environment of horses appears to significantly influence learning abilities may be due, in part, to the impacts these factors can have on the horse's psychological well-being. Given the diversity of roles horses play in different societies and the wide range of rearing and home environments horses can be found in, this suggests that research findings on the cognitive abilities of one population of horses may not be representative of other populations with different life experiences. Further research is needed to clarify how and why these populations differ.

Previous research has demonstrated that individuals exhibiting stereotypic behaviours tend to have stunted learning and problem solving abilities and that the type of stereotypy a horse engages in (such as weaving or cribbing) may influence their behaviour on certain cognitive tasks (Kirsty et al., 2015). Hausberger et al. (2007) found that horses with stereotypic behaviours, such as weaving, cribbing, head shaking, and tongue play, tend to take longer to learn and complete basic tasks, such as pushing open a chest for a food reward, when compared to non-stereotypic horses. Horses with stereotypic behaviour tended to not lie down or sleep as much as non-stereotypic horses, which, as Hausberger et al. (2007) suggests, may lead to lower attention spans and motivation levels that impact a range of behaviours. As a result, stereotypy, a phenomena that can be a health hazard to the horse and is often troubling in terms of husbandry, may be a relevant factor that should be considered when testing horses for learning ability or interpreting cognitive results. Stereotypic horses appear to differ from typically functioning populations and may require specialized training or methodological approaches (Hausberger et al., 2007), a finding that could be relevant to learning disability studies in human psychology. It should be noted that past research suggests a correlation between stereotypic behaviours and the stalling of horses (McGreevy et al., 1995), although the exact relationship between stalling, the display of stereotypic behaviours, and learning ability is still largely unknown.

The duration and method of training may affect a horse's ability to learn. Research has suggested that horses that are trained every day learn faster, have lower average heart rates during training, and make less errors during training than horses that are given breaks (or "days off") during training. This was only found when the horses were subject to complex training systems that required a horse to learn and process multiple pieces of information at once, and seemed to not be true for simple avoidance or association tasks (Kusunose and Yamanobe, 2002). Horses rehabilitated or trained using positive reinforcement (as opposed to negative reinforcement) techniques tend to have lower training times, higher motivation to participate in training, engage in more exploratory behaviour, appear to perceive training and humans (both familiar and unfamiliar) more positively, have increased memory, and display less problem behaviours during training sessions (McCall, 2007; Warren-Smith and McGreevy, 2007; Innes and McBride, 2008; Sankey et al., 2010a, 2010b; Slater and Dymond, 2011). The type of reinforcement used and the training environment appear to play a role in a horse's perception of humans (Sankey et al., 2010c; Baragli et al., 2011) This is consistent with findings in other animals (Desmond and Laule, 1994; Hiby et al., 2004; Laule and Whittaker, 2007).

Horses seem to be profoundly affected by prior positive or negative associations with their human trainer. Sankey et al. (2010b) showed that when horses are taught a simple voice command ("stay") and are then taught to generalize this voice command to different contexts (such as veterinary care and basic handling procedures) using positive reinforcement, those horses engage in more affiliative behaviours with known and unknown humans during training. Horses trained with positive reinforcement are able to respond to the voice command even after eight months of no training and engage in more affiliative behaviours with known and unknown humans outside of training contexts when compared to the control group, which received no reward. This suggests that creating positive affiliations with human trainers is beneficial to both the learning process and the human-horse bond in the long term (Sankey et al., 2010b). A study by Visser et al. (2003) showed that a negative emotional state, as defined by elevated heart rate and engaging in aggressive or anxious behaviours during training (e.g., pawing or vocalizing) may lead to unresponsiveness during training, especially in young horses with little to no prior training experience(Visser et al., 2003). This makes sense in light of a recent study that showed that when horses were under stressful conditions (such as a novel environment) they completed less training stages when taught to step sideways than horses in a home environment (Christensen et al., 2012). Other research has shown similar findings, indicating that a horse's emotional state can influence how well the animal learns, at least in the context of discriminative tasks and reversals and a horse's memory in a delayed-response task (Starling et al., 2013; Valenchon et al., 2013; Mengoli et al., 2014). Horses may have individual preferences for training techniques (Visser et al., 2003). This suggests the need for more individualized training programs for horses, a concept that has been shown in other species, including humans (Visser et al., 2003).

Many animal trainers believe that positive reinforcement appears to be the best training technique from an animal welfare standpoint (Pryor, 1999). Some horse trainers have incorporated this training method, at least partially, in their programs in the form of clicker training (using a secondary reinforcer, such as a clicker or tongue pop, to mark a correct response in a training context prior to the delivery of food or some other positive reinforcer) (Pryor, 1999; Kurland, 2004). Despite this, many horse trainers, handlers, and caretakers rarely use this training method. Cultural traditions surrounding horse training and the belief that this method may not be effective in horses are commonly cited reasons for this choice (McCall, 2007).

While researchers have found ways to use positive reinforcement for basic operant tasks with horses (Sappington and Goldman, 1994; Hanggi, 2003; McCall et al., 2003; Innes and McBride, 2008; Murphy, 2009; Hanggi, 2010b), less empirical research has been done on the effectiveness and outcomes of different training methods more broadly. The research that does exist suggests that many common equine practices, such as farrier work, loading into a trailer, and the reduction of problem behaviours (such as biting) can all be trained using differential positive reinforcement (Slater and Dymond, 2011; Fox et al., 2012). When combined with the evidence that positive reinforcement appears to be beneficial for training and the human-horse relationship (Sankey et al., 2010a), this suggests that some of the popular cultural beliefs surrounding horse trainability may be incorrect and in need of further investigation.

As horses are a typically a ridden animal, in many settings using only positive reinforcement as a training method may present challenges for researchers and trainers alike which may be very difficult to overcome. This is especially true under conditions where negative reinforcement may occur as a natural contingency (e.g., the rider removing equipment or shifting their weight to keep balanced in response to a horse's actions). More user-friendly education about positive and negative reinforcement and the use of riding techniques that correctly maximize horse welfare and human safety may reduce the apparent gap between empirical findings and applied practices. Horse trainers and owners often incorrectly implement negative reinforcement or positive punishment with horses, leading to welfare concerns and behavioural problems – identifying effective strategies to educate owners, handlers and trainers about horse cognition, including the best ways to implement principles from learning theory (and avoid the undesirable side effects associated with aversive control) may be an important direction for future applied research as well as animal behaviour education (McGreevy and McLean, 2007; Ödberg and Gombeer, 2012; Baragli et al., 2015).

One popular training technique or practice gaining traction in the horse community is the idea of "natural" or "sympathetic" horsemanship. This technique allegedly utilizes horse ethology in the hopes of creating a more efficient training program while simultaneously increasing horse welfare (Birke, 2007). Although such methods often imply a scientific approach, the use of scientific terminology in popular training programs is often incorrect and not true to the underlying ethological or scientific findings that they are reportedly borrowed from (McGreevy and McLean, 2007). Nevertheless, some research has suggested that the resulting approaches may still have advantages when compared to conventional training methods. Visser et al. (2009) found that horses trained using conventional methods, which often employ punishment and negative reinforcement techniques, i.e. horse breaking, showed more signs of fear and stress (including higher heart rates during training and future riding) when compared to horses trained using sympathetic horsemanship methods. Likewise, Fureix et al. (2009) found that horses trained for basic handling using natural horsemanship methods were faster in their approach to an unfamiliar person when compared to horses trained with traditional methods. Given that no difference was found between the two groups in terms of their emotional reactivity during handling, the researchers acknowledged that more studies are needed to draw definitive conclusions (Fureix et al., 2009). Recent research has shown that there are differences between breeds in how horses respond to a sympathetic training approach, suggesting that not all horses will respond to a training technique in the same way (Janczarek et al., 2013).

It may be important for future research to define what constitutes traditional versus natural horsemanship. Some, including Birke (2007), suggest that the general methodology employed by natural horsemanship may often be similar to conventional methods; the culture or mindset associated with natural horsemanship may promote positive feelings among human members and encourages them to rely less on tradition alone (Birke, 2007). This is supported by the fact that horse training techniques rely on negative reinforcement, regardless of whether they are sympathetic or not (Baragli et al., 2015), and more research is needed to better discern why one training method appears more effective than another.

There may be less explored downsides to natural horsemanship. This is particularly true given the tendency to emphasize the replication of horse–horse social behaviour during training, which can present the possible danger of encouraging unwanted behaviours with people that horses engage in with conspecifics. This includes rough play-fighting or the aggression that comes when horses establish herd hierarchies (Birke, 2007; McGreevy et al., 2009). Some natural horsemanship approaches capitalize on the notion that horses may perceive humans as predators. The human-horse relationship appears to be more complex than one described as a traditional prey/predator relationship (McGreevy et al., 2009). Birke et al. (2011) showed that the manner in which a human approached a horse affected the horse's flight distance. A direct (as opposed to indirect) approach led to larger flight distances in experienced riding horses. A fast approach lead to greater and faster flight responses in feral ponies. Unlike other vertebrae species, indirect gazing *increased* the horse's reactivity, and tense versus relaxed body posture seemed to have no effect on the horse's flight distance (Birke et al., 2011). The assumption that the human-horse relationship is similar to a traditional predator-prey relationship may be flawed.

Given the wide variety of training techniques used by trainers with their horses, including natural horsemanship, traditional methodology, positive reinforcement or a combination of those (DeAraugo et al., 2014), it is of no surprise that there is much confusion about how horses should be handled, ridden, and trained. Several researchers have suggested that properly utilizing learning theory in horse training and riding (Goodwin et al., 2009; Hawson et al., 2010; McLean and McGreevy, 2010a; Ödberg and Gombeer, 2012; Baragli et al., 2015) as informed by equitation science (Ödberg and Bouissou, 1999; Goodwin et al., 2009; McLean and McGreevy, 2010b) is the most logical approach to maintaining equine welfare and human-horse safety in a variety of contexts. Thus more research is needed to determine what aspects of training, or differences training culture, can account for reported differences in horse and human behaviour where differences exist, as well as possible benefits and downsides of different methods in terms of welfare and the human-horse bond (McGreevy and McLean, 2007). More research evaluating positive reinforcement based methods for horses, including clicker training (Kurland, 2004), is needed, particularly when considering the difficulty in providing positive reinforcement from a riding position (Starling et al., 2013). Here substantial differences are known to exist based on learning theory (when compared with traditional methods), yet empirical studies in this area are limited. This is especially important given evidence that these methods are sometimes less utilized by the general public or, more often, are applied incorrectly (Hockenhull and Creighton, 2013; Baragli et al., 2015).

5.2. Factors affecting horse performance and considerations for future research

Research suggests that a number of individual factors, including sex, breed, social status and genotype, can influence a horse's learning style and abilities. In an experiment done by Murphy et al. (2004), horses were given a task that required them to use depth-based visual cues to obtain food from one of four stalls. Each stall had a food reward that was either accessible to the horse, or not, based on the depth of a wooden board positioned at varying lengths from the reward. When the board was placed at a depth of 1.1 m the horse could obtain the reward, making the stall with this design the optimal choice. In the other stalls, boards were positioned at increasing increments of 0.3 m, such that the horse could not reach food in any of the other stalls. While female horses located the stall with accessible food slightly faster than male horses on the first trial, female performance remained largely unchanged throughout six trials. In contrast, the male horses took longer to solve the task on the first trial but were faster to solve the task than females on all subsequent trials, making fewer errors overall (Murphy et al., 2004). A similar study by Wolff and Hausberger (1996) found that the age of the horse, sex, and the sire did not affect the horse's ability to learn during the relatively simple instrumental task of opening a chest for a food reward. Foals of a particular sire tended to take longer to learn the task, suggesting that genetics may play a role. Mares tended to learn faster than stallions, showing that females may excel at instrumental tasks while males excel at visual-spatial problem solving (Wolff and Hausberger, 1996; Murphy et al., 2004). This may be due, at least in part, to head or eye shape difference between horses, as individuals and breeds can have dramatically different head shapes (e.g., the Arabian) that may influence learning. These findings were supported by a recent study that demonstrated that offspring of certain sires and dams showed higher learning efficiency during target training than offspring from other sires and dams, indicating that genetics do play a role in a horse's learning ability (Bonnell and McDonnell, 2016).

Perceptual abilities interact with study design to influence performance. Multiple studies have found that the placement of stimuli in basic discrimination trials can unintentionally alter success rates. When signals for food are placed above eye level, horses have been shown to be less successful on a basic operant task than when stimuli are placed at or below eye level (Gardner, 1933). When stimuli are placed at ground level, horses are even more successful (Hall, 2007). Likewise, stimuli placed laterally around the horse can lead to enhanced discrimination success, while decrements in performance have been noted when stimuli are placed directly behind, or nearly directly behind, the horse; a finding that makes sense given a horse's blind spots (Hanggi and Ingersoll, 2012). While some hypotheses have been proposed for such outcomes, e.g. horses are less comfortable with their head held high (Hanggi and Ingersoll, 2012), more research is needed to understand these performance trends. Nonetheless, these results demonstrate that placement of stimuli may be a critical consideration when assessing a variety of cognitive abilities in the domestic horse.

It has been suggested that horses may have colour-vision abilities that are similar to humans with red-green colour blindness, making them dichromatic and potentially hinting at problems in the design of discrimination tasks that rely solely on colour (Hanggi et al., 2007). In a study that tested a horse's reaction to a variety of coloured mats, it was found that horses reacted more to mats in yellow, white, blue, and black than mats in grey, brown, green, or red. Interestingly, yellow, white, and black mats elicited more aversive reactions from the animal, but only if the mats were placed on the ground (Hall and Cassaday, 2006). If the mats were placed on the wall, less aversive behaviour was shown (Hall and Cassaday, 2006). This is may be because horses are more likely to attend to stimuli that is at or near ground level in general (Hall, 2007) or this differentiated response could be based on previous experience with similar stimuli (Hall, 2007; Fureix et al., 2009; Sankey et al., 2010c). Horses may have previous experience with differently coloured food buckets, tack, or wall decorations that are often encountered in human environments, leading to some desensitization and less aversion when confronted with the coloured stimulus (Hall and Cassaday, 2006).

Some anecdotal evidence suggests that horses will react differently to a stimulus depending on which side the horse views the stimulus on. Many horse trainers will claim that each side of the horse is a "new side" and that horses are likely to react in novel ways when the sides are switched. Because of this, a common training belief is to ask the horse to approach a human with both eyes, as opposed to one more than the other (Hanggi, 1999). There is no anatomical reason for why horses would be incapable of brain lateralization (Olivares et al., 2001; Aboitiz et al., 2003). Indeed, in what appears to be contradictory evidence to these anecdotal claims, horses were taught a basic discrimination task using a positive visual stimulus and a negative visual stimulus while one eye (right or left) was covered. Horses were able to learn the task with one eye covered and replicate it while the "learning eye" was covered and the untrained eye was uncovered (Hanggi, 1999). Horses could then perform a reversal of the initial task. This would be indicative of interocular transfer, or the ability to transfer information across brain hemispheres (Hanggi, 1999).

Other studies suggest that lateralized emotional processing occurs in the horse, a finding that is consistent with research done on the horse's closest undomesticated relative, Przewalski horses (Austin and Rogers, 2014). Researchers presented horses with positive (a feed bucket the horses were familiar with), neutral (a novel orange cone), and negative (a white coat commonly worn by the barn veterinarian) stimuli. Horses took the longest to approach the negative stimuli, showed a preference to view the neutral stimuli with their right eye, and used their right nostril more often than their left when investigating the neutral and novel object. Horses tended to use their left eye to investigate the negative stimulus and both eyes to investigate the positive stimulus (Deboyerdesroches et al., 2008). Research has indicated that horses appear to prefer to view humans with their left eye; and although horses are traditionally trained on their left side, this finding was found in horses who had been trained from both sides (Farmer et al., 2010). These results may hint at the animal's emotional state while assessing stimuli, a potentially important factor while performing behavioural research on any animal, but in particular on predominantly monocular animals such as horses (Deboyerdesroches et al., 2008; Farmer et al., 2010; Leliveld et al., 2013).

Complicating the problem of testing equine learning ability is the perception that horses lack an ability to focus their attention on any one stimulus for an extended period of time. Research on this has yielded mixed results (McLean, 2004; Murphy, 2009; Whishaw et al., 2009; Hanggi, 2010b). If this is true, it would be in contrast to other animals used in behaviour research, such as dogs, which are often asked to focus their attention on a researcher or human handler for extended periods to accomplish some goal (e.g. Miklósi et al., 2000; Jakovcevic et al., 2012; Udell et al., 2013). Conversely, as is evident with Clever Hans, there are reports that horses are capable of responding to very subtle movements given by human handlers (Pfungst, 1911; Maros et al., 2008b; Dorey et al., 2014), a trait used by trainers and handlers but not well covered by the empirical literature (Hall, 2007). Some have suggested that horses may be strongly driven by survival needs, and have difficulty generalizing learned concepts, particularly those associated with visual or spatial stimuli. Though this has previously been associated with poor learning ability, Hall (2007) suggests it may be due to their biological niche and status as a prey animal, not a lack of intelligence. Given that dogs and cats fill a different niche as scavengers and predators, this may be another important consideration in the design and interpretation of future research, especially for comparative studies.

Both memory and human influence may influence performance on cognitive tasks. McLean (2004) found that when horses were allowed to view and hear the dropping of food into a bucket, they could successfully chose that bucket upon immediate release. Horses did not successfully chose the rewarding bucket after a ten-second delay (McLean, 2004). McLean (2004) notes that people tend to have expectations of their horses in regards to cognitive tasks, and this may have contributed to experimenters inadvertently cuing horses during trials. To test this hypothesis, Murphy (2009) tested horses in a Y-maze apparatus with a food bucket at each end. Horses were allowed to view and hear feed being dropped into the bucket but were delayed in their release for up to 12 s. An apparatus was built that allowed the experimenter who delivered the food to remain out of sight of the horses, while handlers were only involved with collecting the horses after they had been tested and bringing them to the "start" position of the maze, where the horses were then allowed off of their lead ropes but were kept in place by a gate that handlers could open once they stepped away from the horse. Horses were able to solve the problem above chance and improved in subsequent trials, suggesting that horses may have a trainable form of memory (Murphy, 2009). Similarly, Hanggi (2010b) found that horses who were taught to stand without a handler at a start point while viewing feed being dropped into two buckets (with the experimenter who delivered the food hiding behind a board between the buckets during testing trials) could chose the rewarding bucket after a 30 s delay. This was true even when horses attended to distractions in the environment and did not maintain their gaze on the bucket (Hanggi, 2010b).

Study design plays an important role in assessing and interpreting the outcomes of horse behaviour and cognition research. Catering to a horse's prey animal nature, using spatial cues over visual, being mindful of any signals coming from researchers, and placing stimuli near the ground may allow for better and more accurate evaluations of equine cognitive capacity. Researchers should be cautious of anecdotal claims when designing, implementing, and interpreting results regarding equine cognitive abilities, as horses appear to be much more capable of solving complex problems and learning advanced tasks than previously thought.

6. Conclusion

Horse cognition research sometimes yields results that contradict commonly held beliefs about horse cognition and behaviour, and thus common horse management and training techniques (McCall, 2007; McGreevy and McLean, 2007; Murphy and Arkins, 2007). Consequently, greater empirical knowledge could improve horse welfare while simultaneously adding to a base of research that can be used to better understand the horse as a species. This would allow for more comparisons with other animals, particularly companion animals and other grazing ungulates such as cattle and sheep.

It would be folly to not acknowledge that there is difficulty studying an animal such as the horse. While horses themselves may be relatively easy to obtain, their care and housing is much more expensive than typical research animals, often resulting in smaller sample sizes that make drawing definitive conclusions difficult (Cooper, 2007). Researchers can use volunteer subjects, but the public may sometimes be wary of experimentation when it comes to their animals, regardless of whether the research has been approved by an ethical committee or not (Murphy and Arkins, 2007).

It is clear from the empirical work that a horse's background can have dramatic effects on research results, and this can be challenging to control for when using volunteers, unless, as some past researchers have done, only foals are used. This can influence results, as younger horses appear to perform at least somewhat differently on cognitive tasks than older horses. As with the study of any species, scientists may encounter horse-specific limitations or challenges that determine what can and cannot be studied effectively within certain populations. These limitations should not discourage further research, but instead should inform the questions asked and procedural designs used.

More public outreach is needed if extension of scientific findings to applied work is to be achieved; a task that many equine behaviourists report as a challenge (McCall, 2007). This may explain why common beliefs of many horse handlers and trainers – for example, the idea that horses are not good at basic discrimination and generalization tasks, or that positive reinforcement training cannot be employed effectively with this species – are not consistent with the findings of modern scientific research on horse behaviour. Overcoming these problems is not an easy task, but could make an important difference in the understanding, care and welfare of horses and human-horse interactions on a monumental scale. The current research on horse behaviour and cognition has provided an important foundation for what can and should become a rich and exciting area of basic and applied research in years to come.

References

Aboitiz, F., López, J., Montiel, J., 2003. Long distance communication in the human brain: timing constraints for inter-hemispheric synchrony and the origin of brain lateralization. Biol. Res. 36, 89–99.

Ahrendt, L.P., Christensen, J.W., Ladewig, J., 2012. The ability of horses to learn an instrumental task through social observation. Appl. Anim. Behav. Sci. 139, 105–113.

Andrieu, J., Henry, S., Hausberger, M., Thierry, B., 2015. Informed horses are influential in group movements, but they may avoid leading. Anim. Cogn., Available from: http://link.springer.com/10.1007/s10071-015-0945-2.

Austin, N.P., Rogers, L.J., 2014. Lateralization of agonistic and vigilance responses in Przewalski horses (*Equus przewalskii*). Appl. Anim. Behav. Sci. 151, 43–50.

Baer, K.L., Potter, G.D., Friend, T.H., Beaver, B.V., 1983. Observation effects on learning in horses. Appl. Anim. Ethol. 11, 123–129.

Baker, A.E.M., Crawford, B.H., 1986. Observational learning in horses. Appl. Anim. Behav. Sci. 15, 7–13.

Baragli, P., Mariti, C., Petri, L., De Giorgio, F., Sighieri, C., 2011. Does attention make the difference? Horses' response to human stimulus after 2 different training strategies. J. Vet. Behav. Clin. Appl. Res. 6, 31–38.

Baragli, P., Padalino, B., Telatin, A., 2015. The role of associative and non-associative learning in the training of horses and implications for the welfare (a review). Ann. DellIstituto Super. Sanità 51, 40–51.

Birke, L., 2007. "Learning to Speak Horse": The Culture of N̈atural Horsemanship". Anim. Soc. J. Anim.-Hum. Stud. 15 (2007), 217–239.

Birke, L., Hockenhull, J., Creighton, E., Pinno, L., Mee, J., Mills, D., 2011. Horses' responses to variation in human approach. Appl. Anim. Behav. Sci. 134, 56–63.

Blackmore, T.L., Foster, T.M., Sumpter, C.E., Temple, W., 2008. An investigation of colour discrimination with horses (*Equus caballus*). Behav. Processes 78, 387–396.

Bonnell, M.K., McDonnell, S.M., 2016. Evidence for sire, dam, and family influence on operant learning in horses. J. Equine Vet. Sci. 36, 69–76.

Christensen, J.W., Ahrendt, L.P., Lintrup, R., Gaillard, C., Palme, R., Malmkvist, J., 2012. Does learning performance in horses relate to fearfulness, baseline stress hormone, and social rank? Appl. Anim. Behav. Sci. 140, 44–52.

Christensen, J.W., Rundgren, M., Olsson, K., 2006. Training methods for horses: habituation to a frightening stimulus. Equine Vet. J. 38, 439–443.

Clarke, J.V., Nicol, C.J., Jones, R., McGreevy, P.D., 1996. Effects of observational learning on food selection. Appl. Anim. Behav. Sci. 50, 177–184.

Cooper, J.J., 2007. Equine learning behaviour: common knowledge and systematic research. Behav. Processes 76, 24–26.

DeAraugo, J., McLean, A., McLaren, S., Caspar, G., McLean, M., McGreevy, P., 2014. Training methodologies differ with the attachment of humans to horses. J. Vet. Behav. Clin. Appl. Res. 9, 235–241.

Deboyerdesroches, A., Richardyris, M., Henry, S., Ezzaouia, M., Hausberger, M., 2008. Laterality and emotions: visual laterality in the domestic horse (*Equus caballus*) differs with objects' emotional value. Physiol. Behav. 94, 487–490.

Desmond, T., Laule, G.E., 1994. Use of positive reinforcement training in the management of species for reproduction. Zoo Biol. 13, 471–477.

Dorey, N.R., Conover, A.M., Udell, M.A.R., 2014. Interspecific communication from people to horses (*Equus ferus caballus*) is influenced by different horsemanship training styles. J. Comp. Psychol. 128, 337–342.

Dougherty, D.M., Lewis, P., 1991. Stimulus generalization, discrimination learning, and peak shift in horses. J. Exp. Anal. Behav. 56, 97–104.

Farmer, K., Krueger, K., Byrne, R.W., 2010. Visual laterality in the domestic horse (*Equus caballus*) interacting with humans. Anim. Cogn. 13, 229–238.

Fiske, J.C., Potter, G.D., 1979. Discrimination reversal learning in yearling horses. J. Anim. Sci. 49, 583–588.

Flannery, B., 1997. Relational discrimination learning in horses. Appl. Anim. Behav. Sci. 54, 267–280.

Fox, A.E., Bailey, S.R., Hall, E.G., St Peter, C.C., 2012. Reduction of biting and chewing of horses using differential reinforcement of other behavior. Behav. Processes 91, 125–128.

Fureix, C., Pagès, M., Bon, R., Lassalle, J.-M., Kuntz, P., Gonzalez, G., 2009. A preliminary study of the effects of handling type on horses' emotional reactivity and the human–horse relationship. Behav. Processes 82, 202–210.

Gabor, V., Gerken, M., 2012. Cognitive testing in horses using a computer based apparatus. Appl. Anim. Behav. Sci. 139, 242–250.

Gardner, P., 1933. Response of horses to the same signal in different positions. J. Comp. Psychol. 15, 445–467.

Goodwin, D., 2007. Equine learning behaviour: what we know, what we don't and future research priorities. Behav. Processes 76, 17–19.

Goodwin, D., McGreevy, P., Waran, N., McLean, A., 2009. How equitation science can elucidate and refine horsemanship techniques. Vet. J. 181, 5–11.

Hall, C., 2007. The impact of visual perception on equine learning. Behav. Processes 76, 29–33.

Hall, C.A., Cassaday, H.J., 2006. An investigation into the effect of floor colour on the behaviour of the horse. Appl. Anim. Behav. Sci. 99, 301–314.

Hanggi, E.B., 1999. Interocular transfer of learning in horses. J. Equine Vet. Sci. 19, 51–524.

Hanggi, E.B., 2003. Discrimination learning based on relative size concepts in horses (*Equus caballus*). Appl. Anim. Behav. Sci. 83, 201–213.

Hanggi, E.B., 2010a. Rotated object recognition in four domestic horses (*Equus caballus*). J. Equine Vet. Sci. 30, 175–186.

Hanggi, E.B., 2010b. Short-term memory testing in domestic horses: experimental design plays a role. J. Equine Vet. Sci. 30, 617–623.

Hanggi, E.B., Ingersoll, J.F., 2009. Long-term memory for categories and concepts in horses (*Equus caballus*). Anim. Cogn. 12, 451–462.

Hanggi, E.B., Ingersoll, J.F., 2012. Lateral vision in horses: a behavioral investigation. Behav. Processes 91, 70–76.

Hanggi, E.B., Ingersoll, J.F., Waggoner, T.L., 2007. Color vision in horses (*Equus caballus*): deficiencies identified using a pseudoisochromatic plate test. J. Comp. Psychol. 121, 65–72.

Hausberger, M., Gautier, E., Müller, C., Jego, P., 2007. Lower learning abilities in stereotypic horses. Appl. Anim. Behav. Sci. 107, 299–306.

Hausberger, M., Roche, H., Henry, S., Visser, E.K., 2008. A review of the human–horse relationship. Appl. Anim. Behav. Sci. 109, 1–24.

Hawson, L.A., McLean, A.N., McGreevy, P.D., 2010. The roles of equine ethology and applied learning theory in horse-related human injuries. J. Vet. Behav. Clin. Appl. Res. 5, 324–338.

Heitor, F., Vicente, L., 2007. Learning about horses: what is equine learning all about? Behav. Processes 76, 34–36.

Henselek, Y., Fischer, J., Schloegl, C., 2012. Does the stimulus type influence horses' performance in a quantity discrimination task? Front. Psychol. 3, Available from http://journal.frontiersin.org/article/10.3389/fpsyg.2012.00504/abstract.

Hiby, E.F., Rooney, N.J., Bradshaw, J.W.S., 2004. Dog training methods: their use, effectiveness and interaction with behaviour and welfare. Anim. Welf., 63–69, South Mimms Engl.

Hockenhull, J., Creighton, E., 2013. Training horses: positive reinforcement, positive punishment, and ridden behavior problems. J. Vet. Behav. Clin. Appl. Res. 8, 245–252.

Hothersall, B., Gale, E.V., Harris, P., Nicol, C.J., 2010. Cue use by foals (*Equus caballus*) in a discrimination learning task. Anim. Cogn. 13, 63–74.

Innes, L., McBride, S., 2008. Negative versus positive reinforcement: an evaluation of training strategies for rehabilitated horses. Appl. Anim. Behav. Sci. 112, 357–368.

Jakovcevic, A., Mustaca, A., Bentosela, M., 2012. Do more sociable dogs gaze longer to the human face than less sociable ones? Behav. Processes 90, 217–222.

Janczarek, I., Stachurska, A., Kędzierski, W., Wilk, I., 2013. Responses of horses of various breeds to a sympathetic training method. J. Equine Vet. Sci. 33, 794–801.
Keeling, L.J., Jonare, L., Lanneborn, L., 2009. Investigating horse–human interactions: the effect of a nervous human. Vet. J. 181, 70–71.
Kirsty, R., Andrew, H., Meriel, M.-C., Catherine, H., 2015. Cognitive differences in horses performing locomotor versus oral stereotypic behaviour. Appl. Anim. Behav. Sci. 168, 37–44.
Krueger, K., Farmer, K., Heinze, J., 2014. The effects of age: rank and neophobia on social learning in horses. Anim. Cogn. 17, 645–655.
Krueger, K., Flauger, B., 2007. Social learning in horses from a novel perspective. Behav. Processes 76, 37–39.
Krueger, K., Flauger, B., Farmer, K., Maros, K., 2010. Horses (*Equus caballus*) use human local enhancement cues and adjust to human attention. Anim. Cogn. 14, 187–201.
Krueger, K., Heinze, J., 2008. Horse sense: social status of horses (*Equus caballus*) affects their likelihood of copying other horses' behavior. Anim. Cogn. 11, 431–439.
Kurland, A., 2004. Clicker Training for Your Horse. Reissue. Ringpress Books, UK.
Kusunose, R., Yamanobe, A., 2002. The effect of training schedule on learned tasks in yearling horses. Appl. Anim. Behav. Sci. 78, 225–233.
Lampe, J.F., Andre, J., 2012. Cross-modal recognition of human individuals in domestic horses (*Equus caballus*). Anim. Cogn. 15, 623–630.
Lansade, L., Bouissou, M.-F., 2008. Reactivity to humans: A temperament trait of horses which is stable across time and situations. Appl. Anim. Behav. Sci. 114, 492–508.
Lansade, L., Neveux, C., Levy, F., 2012. A few days of social separation affects yearling horses' response to emotional reactivity tests and enhances learning performance. Behav. Processes 91, 94–102.
Laule, G.E., Whittaker, M., 2007. Enhancing nonhuman primate care and welfare through the use of positive reinforcement training. J. Appl. Anim. Welf. Sci. 10, 31–38.
Leliveld, L.M.C., Langbein, J., Puppe, B., 2013. The emergence of emotional lateralization: evidence in non-human vertebrates and implications for farm animals. Appl. Anim. Behav. Sci. 145, 1–14.
Lesimple, C., Sankey, C., Richard, M.A., Hausberger, M., 2012. Do horses expect humans to solve their problems? Front. Psychol. 3, Available from: http://journal.frontiersin.org/article/10.3389/fpsyg.2012.00306/abstract.
Lindberg, A.C., Kelland, A., Nicol, C.J., 1999. Effects of observational learning on acquisition of an operant response in horses. Appl. Anim. Behav. Sci. 61, 187–199.
Lovrovich, P., Sighieri, C., Baragli, P., 2015. Following human-given cues or not? Horses (*Equus caballus*) get smarter and change strategy in a delayed three choice task. Appl. Anim. Behav. Sci. 166, 80–88.
Maros, K., Gácsi, M., Miklósi, Á., 2008a. Comprehension of human pointing gestures in horses (*Equus caballus*). Anim. Cogn. 11, 457–466.
Maros, K., Pongrácz, P., Bárdos, G., Molnár, C., Faragó, T., Miklósi, Á., 2008b. Dogs can discriminate barks from different situations. Appl. Anim. Behav. Sci. 114, 159–167.
Martin, T.I., Zentall, T.R., Lawrence, L., 2006. Simple discrimination reversals in the domestic horse (*Equus caballus*): effect of discriminative stimulus modality on learning to learn. Appl. Anim. Behav. Sci. 101, 328–338.
Maurstad, A., Davis, D., Cowles, S., 2013. Co-being and intra-action in horse-human relationships: a multi-species ethnography of be(com)ing human and be(com)ing horse: co-being and intra-action in horse-human relationships. Soc. Anthropol. 21, 322–335.
McBride, S.D., Mills, D.S., 2012. Psychological factors affecting equine performance. BMC Vet. Res. 8, 180.
McCall, C.A., 2007. Making equine learning research applicable to training procedures. Behav. Processes 76, 27–28.
McCall, C.A., Salters, M.A., Johnson, K.B., Silverman, S.J., McElhenney, W.H., Lishak, R.S., 2003. Equine utilization of a previously learned visual stimulus to solve a novel task. Appl. Anim. Behav. Sci. 82, 163–172.
McGreevy, P.D., Cripps, P.J., French, N.P., Green, L.E., Nicol, C.J., 1995. Management factors associated with stereotypic and redirected behaviour in the Thoroughbred Horse. Equine Vet. J. 27, 86–91.
McGreevy, P.D., McLean, A.N., 2007. Roles of learning theory and ethology in equitation. J. Vet. Behav. Clin. Appl. Res. 2, 108–118.
McGreevy, P.D., Oddie, C., Burton, F.L., McLean, A.N., 2009. The horse–human dyad: can we align horse training and handling activities with the equid social ethogram? Vet. J. 181, 12–18.
McKinley, J., Sambrook, T.D., 2000. Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). Anim. Cogn. 3, 13–22.
McLean, A.N., 2004. Short-term spatial memory in the domestic horse. Appl. Anim. Behav. Sci. 85, 93–105.
McLean, A.N., McGreevy, P.D., 2010a. Horse-training techniques that may defy the principles of learning theory and compromise welfare. J. Vet. Behav. Clin. Appl. Res. 5, 187–195.
McLean, A.N., McGreevy, P.D., 2010b. Ethical equitation: capping the price horses pay for human glory. J. Vet. Behav. Clin. Appl. Res. 5, 203–209.
Mengoli, M., Pageat, P., Lafont-Lecuelle, C., Monneret, P., Giacalone, A., Sighieri, C., Cozzi, A., 2014. Influence of emotional balance during a learning and recall test in horses (*Equus caballus*). Behav. Processes 106, 141–150.
Merkies, K., Sievers, A., Zakrajsek, E., MacGregor, H., Bergeron, R., von Borstel, U.K., 2014. Preliminary results suggest an influence of psychological and physiological stress in humans on horse heart rate and behaviour. J. Vet. Behav. Clin. Appl. Res. 9, 242–247.
Miklósi, A., Polgárdi, R., Topál, J., Csányi, V., 2000. Intentional behaviour in dog-human communication: an experimental analysis of showing behaviour in the dog. Anim. Cogn. 3, 159–166.
Miller, R.M., 1995. The amazing memory of the horse. J. Equine Vet. Sci. 15, 340–341.
Murphy, J., 2009. Assessing equine prospective memory in a Y-maze apparatus. Vet. J. 181, 24–28.
Murphy, J., Arkins, S., 2007. Equine learning behaviour. Behav. Processes 76, 1–13.
Murphy, J., Waldmann, T., Arkins, S., 2004. Sex differences in equine learning skills and visuo-spatial ability. Appl. Anim. Behav. Sci. 87, 119–130.
Nicol, C.J., 2002. Equine learning: progress and suggestions for future research. Appl. Anim. Behav. Sci. 78, 193–208.
Ninomiya, S., 2007. Social leaning and stereotypy in horses. Behav. Processes 76, 22–23.
Ödberg, F.O., Bouissou, M.-F., 1999. The development of equestrianism from the baroque period to the present day and its consequences for the welfare of horses. Equine Vet. J. 31, 26–30.
Ödberg, F.O., Gombeer, L., 2012. Old masters were right: academic riding principles abide modern learning theory. J. Vet. Behav. Clin. Appl. Res. 7, e12.
Olivares, R., Montiel, J., Aboitiz, F., 2001. Species differences and similarities in the fine structure of the Mammalian Corpus Callosum. Brain. Behav. Evol. 57, 98–105.
Parelli, P., Kadash, K., Parelli, K., 1993. Natural horse-man-ship. In: Western Horseman. Colorado Springs, CO.
Pfungst, O., 1911. Clever Hans (The horse of Mr. Von Osten): a contribution to experimental animal and human psychology. 2010 Translated Edition, from German, by Carl L. Rhan. Project Gutenberg E-Book, Available from: http://www.gutenberg.org/files/33936/33936-h/33936-h.htm.
Proops, L., McComb, K., 2010. Attributing attention: the use of human-given cues by domestic horses (*Equus caballus*). Anim. Cogn. 13, 197–205.
Proops, L., McComb, K., 2012. Cross-modal individual recognition in domestic horses (*Equus caballus*) extends to familiar humans. Proc. R. Soc. B Biol. Sci. 279, 3131–3138.
Proops, L., Rayner, J., Taylor, A.M., McCom, K., 2013. The responses of young domestic horses to human-given cues, Available from: http://dx.plos.org/10.1371/journal.pone.0067000.
Proops, L., Walton, M., McComb, K., 2010. The use of human-given cues by domestic horses, *Equus caballus*, during an object choice task. Anim. Behav. 79, 1205–1209.
Pryor, K., 1999. Don't Shoot the Dog!: The New Art of Teaching and Training, Revised ed. Bantam, New York.
Rivera, E., Benjamin, S., Nielsen, B., Shelle, J., Zanella, A.J., 2002. Behavioral and physiological responses of horses to initial training: the comparison between pastured versus stalled horses. Appl. Anim. Behav. Sci. 78, 235–252.
Rochais, C., Henry, S., Sankey, C., Nassur, F., Góracka-Bruzda, A., Hausberger, M., 2014. Visual attention, an indicator of human-animal relationships? A study of domestic horses (*Equus caballus*). Front. Psychol. 5, Available from: http://journal.frontiersin.org/article/10.3389/fpsyg.2014.00108/abstract.
Rørvang, M.V., Ahrendt, L.P., Christensen, J.W., 2015. Horses fail to use social learning when solving spatial detour tasks. Anim. Cogn. 18, 847–854.
Sankey, C., Henry, S., André, N., Richard-Yris, M.-A., Hausberger, M., 2011. Do horses have a concept of person?, Available from: http://dx.plos.org/10.1371/journal.pone.0018331.
Sankey, C., Henry, S., Górecka-Bruzda, A., Richard-Yris, M.-A., Hausberger, M., 2010a. The way to a man's heart is through his stomach: what about horses? In: Chapouthier, G. (Ed.), PLoS One 5, e15446.
Sankey, C., Richard-Yris, M.-A., Henry, S., Fureix, C., Nassur, F., Hausberger, M., 2010b. Reinforcement as a mediator of the perception of humans by horses (*Equus caballus*). Anim. Cogn. 13, 753–764.
Sankey, C., Richard-Yris, M.-A., Leroy, H., Henry, S., Hausberger, M., 2010c. Positive interactions lead to lasting positive memories in horses, *Equus caballus*. Anim. Behav. 79, 869–875.
Sappington, B.F., Goldman, L., 1994. Discrimination learning and concept formation in the Arabian horse. J. Anim. Sci. 72, 3080–3087.
Sappington, B.F., McCall, C.A., Coleman, D.A., Kuhlers, D.L., Lishak, R.S., 1997. A preliminary study of the relationship between discrimination reversal learning and performance tasks. Appl. Anim. Behav. Sci. 53, 157–166.
Slater, C., Dymond, S., 2011. Using differential reinforcement to improve equine welfare: shaping appropriate truck loading and feet handling. Behav. Processes 86, 329–339.
Smith, A.V., Proops, L., Grounds, K., Wathan, J., McComb, K., 2016. Functionally relevant responses to human facial expressions of emotion in the domestic horse (*Equus caballus*). Biol. Lett. 12, 20150907.
Søndergaard, E., Ladewig, J., 2004. Group housing exerts a positive effect on the behaviour of young horses during training. Appl. Anim. Behav. Sci. 87, 105–118.
Starling, M., Branson, N., Cody, D., McGreevy, P., 2013. Conceptualising the impact of arousal and affective state on training outcomes of operant conditioning. Animals 3, 300–317.
Stone, S.M., 2010. Human facial discrimination in horses: can they tell us apart? Anim. Cogn. 13, 51–61.
Thomas, R.K., 1986. Vertebrate intelligence: a review of the laboratory research. In: Hoage, R.J., Goldman, L. (Eds.), Animal Intelligence: Insights into the Animal Mind. Smithsonian Institution Press, Washington, DC, pp. 37–56.

Thompson, K., McGreevy, P., McManus, P., 2015. A critical review of horse-Related risk: a research agenda for safer mounts, riders and Equestrian cultures. Animals 5, 561–575.
Topál, J., Miklósi, Á., Csányi, V., 1997. Dog–human relationship affects problem solving behavior in the dog. Anthrozoos Multidiscip. J. Interact. People Anim. 10, 214–224.
Udell, M.A.R., Dorey, N.R., Wynne, C.D.L., 2010. What did domestication do to dogs? A new account of dogs' sensitivity to human actions. Biol. Rev. 85, 327–345.
Udell, M., Hall, N.J., Morrison, J., Dorey, N.R., Wynne, C.D.L., 2013. Point topography and within-session learning are important predictors of pet dogs' (*Canis lupus familiaris*) performance on human guided tasks. Rev. Argent. Cienc. Comport. 5, 3–20.
Uller, C., Lewis, J., 2009. Horses (*Equus caballus*) select the greater of two quantities in small numerical contrasts. Anim. Cogn. 12, 733–738.
Valenchon, M., Lévy, F., Fortin, M., Leterrier, C., Lansade, L., 2013. Stress and temperament affect working memory performance for disappearing food in horses, *Equus caballus*. Anim. Behav. 86, 1233–1240.
Visser, E.K., VanDierendonck, M., Ellis, A.D., Rijksen, C., Van Reenen, C.G., 2009. A comparison of sympathetic and conventional training methods on responses to initial horse training. Vet. J. 181, 48–52.
Visser, E.K., Van Reenen, C.G., Schilder, M.B.H., Barneveld, A., Blokhuis, H.J., 2003. Learning performances in young horses using two different learning tests. Appl. Anim. Behav. Sci. 80, 311–326.
Warren-Smith, A., McGreevy, P.D., 2007. The use of blended positive and negative reinforcement in shaping the halting reponse of horses (*Equus caballus*). Anim. Welf., 481–488.
Whishaw, I.Q., Sacrey, L.-A.R., Gorny, B., 2009. Hind limb stepping over obstacles in the horse guided by place-object memory. Behav. Brain Res. 198, 372–379.
Wolff, A., Hausberger, M., 1996. Learning and memorisation of two different tasks in horses. Appl. Anim. Behav. Sci. 46, 137–143.
Zentall, T.R., 1996. An analysis of imitative learning in animals. In: Heyes, C.M., Galef Jr., B.G. (Eds.), Social Learning in Animals: The Roots of Culture. Academic Press, Inc., pp. 221–244.