

MOTIVATION, STRESS AND LEARNING – CRITICAL CHARACTERISTICS THAT INFLUENCE THE HORSES' VALUE AND TRAINING METHOD – A REVIEW*

Katarzyna Olczak*, Jacek Nowicki, Czesław Klocek

Institute of Animal Science, Department of Swine and Small Animal Breeding, University of Agriculture, al. Mickiewicza 24/28, 30-059 Kraków, Poland *Corresponding author: olczakkasia@gmail.com

Abstract

Equine husbandry is carried out in an environment unnatural to horses, which enforces their adaptation to artificial conditions. Besides housing conditions, the management and human-horse relationship is very important for both human safety and a high level of animal welfare and performance. This would not be possible if horses were not able to learn. For equestrians, independently of the horse's use (sport, work, recreation, therapy etc.) the performance is of the highest importance. Deep knowledge about learning mechanisms is essential to maintain high level of horses' welfare and to achieve effective training. Cognition can be influenced by motivation and stress. Motivational mechanisms are based on positive or negative reinforcement but still it is not known what motivates horses more and how food motivation influences learning. It was already shown that a low level of motivation decreases animal performance. The effect of stress is an increasingly popular research topic. It has been shown that acute stress decreases horses' learning performance, but the exact standard is still unknown. The Yerkes-Dodson law claims that low and too high arousal decreases learning. What is more, the relation between learning and sex, breed and some temperamental traits has been shown in several studies.

Key words: horse, learning, motivation, stress, fearfulness, behavior

Horses are mainly used in sports, for recreation, as draught animals, and sometimes they are just kept for companionship or for their beauty. This variety of tasks enforced the need for adaptation to live and act in artificial conditions. Horses are also forced to perform unnatural behaviors unlike what occurs in nature. For example, instinctively horses would rather go around high obstacles than jump over them, as seen at jumping competitions (McCall, 1990). Furthermore, due to the equine industry, the method of horse transportation, in dark, small trailers, contrary to their

^{*}Article partially supported from BM 4250/15.

instincts, is unavoidable. Working horses need to learn how to respond to various signals to meet expectations (get reward or avoid punishment), and at the same time to discriminate among diverse environmental stimuli. The huge amount of stimulus is neutral and riders train horses to ignore them to avoid sudden fear reactions that can be dangerous. Furthermore, horses naturally learn to ignore neutral stimulus to save energy for real danger in future. Therefore, from a human point of view, horses' learning abilities represent the most important aspects that determine their usefulness. To ensure equine welfare it is necessary to understand their body language, behavioral needs and learning mechanisms. Thus, the amount of research focused on horses' learning abilities increases year by year. These studies are focused on different learning aspects from classical (Lansade et al., 2013) and operant conditioning (Valenchon et al., 2013 a), through discrimination tasks (Martin et al., 2006), spatial learning (McCall, 1990), social learning and learning through social observation (Rørvang et al., 2015; Nicol, 2006). It is suggested that there are differences in horses' behavior due to sex (Wolff and Hausberger, 1996), breed (Hori et al., 2013), and temperamental traits (Lansade and Simon, 2010; Valenchon et al., 2013 a; Valenchon et al., 2013 c). Janczarek et al. (2014) suggests that, according to the breed, horses differ in their level of training ability and that is the reason why it is important to find optimal schooling methods. McGreevy and McLean (2010) indicate that predispositions to learning and training are shaped from early life. The interaction among breed, maternal behavior, weaning method, nutrition, housing, early learning, training and individual differences determine horses' behavior (McGreevy and McLean, 2010). Furthermore, central nervous system coordinates cognition, internal physiology and external behavior. For example, a state of fear shows an excitation of escape, avoidance or freezing and at the same time inhibits other behaviors. The occurrence of strong stressors often inhibits eating and diverts horse attention from signals given from trainers, lowering learning capability (Lansade et al., 2012). It is important to distinguish this aspect from usage of aversive stimulus during training. Aversive, meaning unpleasant, but not eliciting fear reaction. In nature horses learn to avoid aversive stimuli, so this reaction is used in training, and aversiveness, when used with absolute adherence to the principles of learning theory, does not limit learning abilities (McGreevy and McLean, 2010).

It is a common belief that stress is a significant modulator of cognition (Berridge, 2001). Stress in equitation cannot be discussed excluding horses' reactivity and fearfulness, as they are very reactive to many environmental stimuli. Horses evolved as prey animals, whose survival tactic was to escape from predators (Goodwin, 1999). Calabrese (2008) indicates that low levels of arousal is essential for effective trainings. On the other hand, few studies show positive impact of stress on learning (Valenchon et al., 2013 c) and its relation to temperament (Valenchon et al., 2013 a). Therefore fearfulness is the second most important aspect of horse management, due to its impact on humans and horse safety (Hawson et al., 2010).

Arousal level is strongly connected with motivation. Lorenz (1966) thought of motivation as an accumulation of action-specific energy that is released when action occurs (Broom and Fraser, 2007). Such a theory may mean that high arousal level may release such "energy" and make the animal more efficient in adaptation and

thus in learning. On the other hand, stressed animals may have lower perceptual thresholds for relevant stimuli (Aarts et al., 2001). There is a wide range of stressors which affect animals in different life experiences including physical stress, social stress, nutritional stress etc. However, there is no simple explanation how stress influences animals' ability to learn and remember (Schwabe et al., 2012). Adrenal hormones (i.e., catecholamines and glucocorticoids) are secreted during stressful events and affect the organism's ability to cope with stress. These hormones also affect memory function by influences on limbic brain structures. It is well established that adrenal catecholamines promote consolidation and/or storage of novel information (Roozendaal, 2002). Stress and the hormones and neurotransmitters released in response to stress, such as glucocorticoids and catecholamines, shape memory processes. It was confirmed that the effect of stress on learning abilities depends on the time of stressor action. Stress prior to learning can facilitate or reduce memory (Elzinga et al., 2005; Schwabe et al., 2008). Stress immediately after learning enhances memory (Cahill, 2003; Roozendaal, 2000) whereas stress shortly before testing has mainly detrimental effects on memory (Buchanan et al., 2006). Schwabe and Wolf (2010) showed that stress during learning in humans, i.e. during the early phase of the stress response, can have negative effects on subsequent memory performance. They gave the explanation that stress acted as a distractor during encoding, diverting attention from the learning material. Joëls et al. (2006) also reviewed that the direction of changes in memory performance - improvement or impairment - depends on whether the stress experienced is closely linked in time to and within the context of the information to be learned.

Moreover, in human psychology there is a great interest in aspects of motivation. It is well known that motivation plays a crucial role in the aspect of learning and achieving success (McClelland, 1987). Christensen et al. (2012) highlights the paradox that most of learning tests are based on positive reinforcement (food), while most of trainings are based on negative reinforcement. It is still not clear what motivates horses most but some basic mechanisms will be described further.

Learning abilities, motivation and stress are the most important factors that influence horses' performance, management and value. Understanding the underlying mechanisms of those factors seems essential for both equine practitioners and scientists.

Learning mechanisms

Learning is a process of acquiring new information or modifying old ones, leading to new behavior or changed behavior (McGreevy, 2004). Broom and Fraser (2007) gave the following definition: "Learning is a change in the brain, which results in behavior being modified for longer than a few seconds, as a consequence of information from outside the brain". There is a wide range of situations where learning occurs. This means that it is frequent and involved in almost all aspects of behavior. The brain mechanisms that make learning possible include very complex processes in which there is awareness of what is occurring, what has occurred and what is likely to occur (Broom and Fraser, 2007). Different parts of the nervous system are involved in the act of learning. Firstly, the information is processed by senses which receive stimuli from the environment. For example, the sense of touch is involved in gaining information about aversiveness of certain environmental elements (e.g. electric fences) and of positive ones (e.g. mutual grooming). The lips and the whiskers are an important organ of equine touch (Adamczyk et al., 2015). Equine hearing range is 55 Hz to 33.5 kHz, but they are the most sensitive to sounds in the range from 1 to 15 kHz (McGreevy, 2004, reviewed by Adamczyk et al., 2015), that is why high-pitched sounds can be used as punishment during training. Horses' vision acuity and colour discrimination is poor compared with humans, however they are able to see better in light-limited conditions, and they have almost panoramic vision and binocular transfer of optical cues (reviewed by Murphy et al., 2009). Secondly, the information goes through the nervous system to the cerebral cortex, where it is processed and stored.

The change of a few psychobiological functions (such as attention, motivation, information processing and integration of sensory or motor functions) may have an impact on acquisition. What is more, all of these functions can be influenced by stress (Sandi and Pinelo-Nava, 2007). It was observed that fear reaction can be conditioned after one trial only (McGreevy, 2004). Corticosterone has a positive impact on memory consolidation (Sandi and Pinelo-Nava, 2007). Nevertheless, attention and motivation can be diverted from the desirable by the trainer to instinctive fear reaction (Christensen, 2013) (for example: a trainer while working with a horse will use a rain tension expecting a horse to stop – usually the horse is motivated to avoid pressure – the sudden stressful event may divert horse motivation from halt to flight response). One of the techniques to decrease this phenomenon is habituation. The horse is repetitively exposed to frightening stimuli until the undesirable reaction disappears. Habituation is important mostly due to safety reasons. But, as mentioned above, also because a high level of reactivity to the surroundings inhibits learning and memory (Christensen, 2013).

There are many types of learning and thus several training methods. Generally learning can be divided into associative and non-associative. Associative learning occurs when stimuli are associated with time or space (classical or operant conditioning), while non-associative learning results in either habituation or sensitization to single stimuli (McGreevy and McLean, 2010).

Training usually involves instrumental or operant conditioning. Horses' responses are followed by reinforcement or punishment. Reinforcement increases the behavior occurrence, frequency, duration, magnitude or decreases its latency. The reinforcement is used to strengthen the behavior while the punishment lessens it (Christensen et al., 2012).

Reinforcement can be positive (when a pleasant stimulus is applied, e.g. food reward) or negative (when an aversive stimulus, e.g. pressure, is removed) both to reward a desired response (Mills et al., 2010). Negative reinforcement is the most popular method used in classical riding as well as in nowadays popular natural horsemanship. Freymond et al. (2014) found that during the training exercises, mares with negative reinforcement experienced more negative emotions than mares treated with positive reinforcement. Negatively reinforced mares afterwards were in a more optimistic mood compared with positively treated mares, despite previously expe-

riencing more negative emotions during the treatment. An example of positive reinforcement in practice is clicker training, very popular in dog's training, more and more common among equestrians. Horses are trained to follow a target for a reward. Firstly a click as a secondary reinforcement is followed by food (primary reinforcement). This process is an example of typical classical conditioning. After learning process the clicker becomes the primary reward and target can be introduced (the click is a reward for touching the target). What is more, this method is often used to overcome stress while a horse is taught a new stressful task, for example entering a trailer. Hendriksen et al. (2011) has shown that horses trained with positive reinforcement to enter trailer have learnt faster and expressed less signs of stress than horses trained with negative reinforcement. The correlation between the effectiveness of clicker training and horses' food motivation or fearfulness has not been shown yet. It is presumed that some horses will learn better with positive reinforcement, while others with negative reinforcement, which is also task dependent. For instance a very crucial phase in horse training is learning to tolerate being ridden. Such procedure is often called "breaking". Harsh breaking methods simply lead to very poor welfare. Other animal-friendly methods should replace mentioned harsh training, but the age at which horses are trained for riding in races has a great effect on their welfare. Young horses which run fast and frequently on hard ground may suffer from inadequate bone development and thus locomotor anomalies and pain (Broom and Fraser, 2007). A better understanding of this issue will help to apply the correct training to individual horse predispositions and this requires further investigation.

Both classical and natural riding schools use negative reinforcement during horse training. This is in accordance with signals that horses give to each other in nature. Horses' performance in tests with negative reinforcement may reflect their real use-fulness to work. Ahrendt et al. (2015) proposed a standardized test to measure learning abilities with negative reinforcement. Using the same test by scientists and practitioners will provide valuable information about horses' predispositions for learning.

Janczarek et al. (2014) suggest that susceptibility to natural training differs between breeds. Naïve horses were used in this test. The initial training in a round-pen was conducted by a licensed trainer of natural horsemanship. Horses were taught to avoid pressure, walk on a line and were familiarized with novel objects. Authors have found that thoroughbreds are the best, Purebred Arabians rank second and Angloarabians rank lowest. There are probably more factors that determine learning abilities in horses. These findings along with the lack of correlation among different learning tests (e.g. Lansade and Simon, 2010; Visser et al., 2003; Wolff and Hausberger, 1996) suggests that other traits (e.g. motivation, attention, fearfulness) may determine horses' performance in learning tests (Nicol, 2002).

Stress and fearfulness influence learning

The Yerkes-Dodson law says that some level of mental arousal is required to provide an effective performance, but beyond some level it has an opposite effect. This relation can be illustrated by an inverted U-shaped curve (Mendl, 1999). The way animals respond to stress can differ due to several factors like temperament, character, age, sex, or life experience. In the context of learning, working memory requires high levels of energy and superior concentration, thus performance usually decreases under stressful conditions (Mendl, 1999). Probably both temperament and stress (negative and chronic) can affect working memory (Valenchon, 2013 c). It was observed that more anxious mice and students performed better in neutral conditions, but under stressful conditions their performance decreased (Mendl, 1999). Valenchon (2013 c) found similar interactions between horse temperament and performance, which is described further. Mendl (1999) suggests that the impact of stress may impair the true picture of the cognitive abilities of farm animals, as during tests it is often hard to eliminate the stressful stimuli from the environment. Moreover, chronic stress can cause structural and functional brain changes, leading to reduction in animals' learning capacity (Sandi and Pinelo-Nava, 2007).

Only a few studies show the influence of acute stress on horse learning abilities. Valenchon et al. (2013 c) showed that horses exposed to stressors prior to tests performed better learning in tasks like touching targets or moving forward/backward in accordance with the Yerkes-Dodson law (Mendl, 1999). Still further research is required to find the level of arousal that is necessary to improve horses' learning abilities. However, the negative influence of acute stress on learning abilities in horses was also observed. In the study of Valenchon et al. (2013 c) conceptual learning was involved: two buckets were presented to a horse. As it observed, one bucket was baited with food. After an enforced delay, the horse was released and had to choose between two buckets. The results reveal that stress decreased the time of possible delay during which horses still performed correctly. In the same study it was observed that fearful horses were superior in neutral conditions but under stressful situation non-fearful individuals performed better (Valenchon et al., 2013 c). Although Lansade et al. (2012) showed that short isolation of young horses decreased their reactivity, horses become less stressed, which improved their learning abilities. The study of Mengoli et al. (2014) has shown that horses treated with Equine Appeasing Pheromone were characterized by higher attention, lower sensitivity to environmental stimuli, and better learning performance than the control group.

Trainers try various methods to overcome horses' strong fear reaction, such as flight response. The most common techniques of desensitization are: habituation (described earlier), overshadowing, and counter-conditioning techniques. Overshadowing occurs when two stimuli occur at the same time; one is more salient and overshadows the influence of the second one. McLean (2008) describes advantages of this method (for example it enables controlling fear reaction) and suggests that more research should focus on this phenomenon to popularize and apply it in practice. In the mentioned McLean experiment the trained locomotor response was used to overshadow aversive stimulus. It is suggested that this method combined with counterconditioning can be the most effective (McGreevy and McLean, 2010). Counterconditioning is based on classical conditioning mechanisms: the aversive stimulus is used to foreshadow the pleasant stimuli (McGreevy, 2004). For example if a horse is afraid of rustling, the noise can be made just before feeding. The aversive stimulus becomes more attractive. In gradual habituation a horse is exposed to the stressor, but in contrast to overshadowing techniques, not allowed to prevent the horse's fear reaction (Gough, 1999).

The fearful and active horses perform well at avoidance tasks (Lansade and Simon, 2010), which probably correlates with their natural instinct of flight response. There is a chance that those horses will be good for jumping as the best way to avoid aversive stimulus (e.g. leg pressure or rain tension) during training is to jump over. Furthermore, less reactive individuals performed better in instrumental, spatial and discrimination tasks (Lansade et al., 2013; Valenchon et al., 2013 b). Visser et al. (2003) suggest that horse temperamental traits may determine predispositions to react more wanted on specific stimulus/reinforcement. The correlation between temperament and motivation to respond on different reinforcements has not been evaluated.

In behavioral studies the heart rate is commonly used not only to evaluate sport horses but mostly to assess their emotional reaction (Leiner and Fendt, 2011; von Lewinski et al., 2013; Christensen, 2012; Visser et al., 2008). To make research more reliable, hormonal analysis also becomes essential in modern research. Saliva cortisol measurement is very functional because it is a very simple and non-invasive procedure (Wang et al., 2014). This methodology is already commonly used to assess horses' stress levels (Leiner and Fendt, 2011; von Lewinski et al., 2013; Schmidt et al., 2010; Valenchon, 2013). Sometimes, especially in wild animals or during long term research, the fecal cortisol can be measured (Christensen et al., 2012; Schmidt et al., 2010).

Rothman et al. (2014) underlines the lack of practicality of behavioral tests that are used in science. On the other hand, those tests provide the possibility to expand knowledge in a more standardized environment. Rothman's research showed that horses described as reactive by riders/owners were scored the same using behavioral tests. This result suggests that people working with horses have an ability to evaluate temperament correctly. On the other hand, Mills (1998) showed low correlation between standardized test results and trainers' evaluation. Low but significant negative correlation was found between the reactivity of horses and their performance in jumping, but there was no such evidence in the case of dressage (Rothman et al., 2014; Visser et al., 2003). Numerous additional factors may have influenced the results, because the tests were carried out on horses from different stables, trained by different people, and not all of the horses were trained the same amount of time. To confirm the results of Rothman et al. (2014) more research in standardized conditions should be done.

What is more, Hausberger et al. (2007) showed that stereotypic horses were more unsuccessful than non-stereotypic ones. What is more, the stereotypic horses that performed correctly still needed more time to solve the task than non-stereotypic ones. This phenomenon might have been related to frustration.

Motivation

Motivation can be defined as the state of willingness, through physiological and psychological processes, to undertake and sustain certain activities. Motivation can be internal or/and external, where the factor that triggers the specific behavior is a desired result of action (McClelland, 1987). Increased levels of dopamine influence the rewarding system that leads to positive sensations in the brain (Berridge, 2001). Both

positive and negative reinforcement result in dopaminergic system activation. If the reward is used to increase the occurrence of behavior, it works as positive reinforcement and may acquire motivational function. If negative reinforcement is used, the result of behavior is a relief from an aversive stimulus (McClelland, 1987; Berridge, 2001). It has been shown that animals can learn to press a lever in expectation to get a reward. This instrumental task is a common tool to assess animals' motivation. The motivational strength of stimuli can vary in time and may be changed by: ontogeny and age, phylogeny, learning, brain damage and chemical factors (Toates, 2004). Some variables, like metabolic or sexual hormones can influence cognitive processes and modulate the effectiveness of incentive stimuli, depending on the physiological state of the animal. For example the energy deprivation causes increased motivational value of food. In contrast, when animals meet their nutritional needs but suffer from water deprivation food may be less attractive than water. The lack of one element (desire or the result) causes no motivational effect of the other even if it is very intensive (Berridge, 2001). Very strong motivation can induce frustration if an animal does not have the possibility to meet its needs or the reward is terminated (Held et al., 2009). In addition, the neutral stimuli, if connected with reward, can acquire the incentive value (through classical conditioning). It can work not only as a prediction of upcoming reward, but may also gain capacity to evoke emotions and motivation. The stimuli become attractive and work as conditional reinforcement. In learning theory it is called secondary reinforcement (Flagel et al., 2010). Robinson and Flagel (2009) showed that there is a difference in the way animals make associations. Some rats learned the operational task quickly, because they pressed the lever and then went to the bowl to achieve the reward, while others were not able to associate lever with reward and went to the bowl without pressing the lever. Furthermore, in laboratory conditions it was observed that "free" rewards can be very effective incentives when given at the beginning or when the animal is losing interest. Often the first response is very weak until an animal gets a first reward or just a "free" reward (Berridge, 2001).

What is more, stress may have negative impact not only on learning abilities but also on motivational processes. If the problem is too hard for an animal and it takes too long to solve it the signs of frustration are observed. If the situation repeats or is extended, learned helplessness may occur. This phenomenon causes a decrease in dopamine level and blocks the desire of reward that results in lack of motivation (Berridge, 2001). For example some individuals in stressful conditions may not respond to food, while in neutral situations the food seems to be a good reward for them. However, it can also be seen that food is used by trainers to shift horses attention from aversive stimulus to food.

It is suggested that food has a great incentive value for horses, especially those kept in stables with limited food access. The act of eating is a positive sensation for horses, as in nature they spend most of the day on grazing (Ninomiya et al., 2007). In equine science food is often used as a reward in different behavioral tests, but in practice the negative reinforcement is much more common (Nicol, 2002). In addition, in the fear tests, it is very common to measure the time from the point a stressor is applied to the moment a horse resumes eating (Christensen et al.,

2012; Lansade and Simon, 2010 a; Valenchon et al., 2013 c). It seems logical that more reactive horses with strong motivation towards food may start to eat quicker than less fearful horses with low food motivation. But this requires further investigation.

Motivation is crucial to achieve success, nevertheless there is a lack of scientific knowledge about food motivation in horses and its correlation with equine behavior and learning abilities. Food motivation is only mentioned in few studies. For example Lindberg et al. (1999) paid attention to the way horses were fed to make sure that all had the same level of food motivation in concept of hunger. The result showed that non warmblood horses performed better, which could be caused by lower reactivity of these horses, or by higher levels of motivation for seeking out food, or both. Ponies evolved in an environment with limited sources of food that forced them to look for new solutions of gaining food example (Lindberg et al., 1999). Most warmblood horses were kept intensively for centuries, which could cause the decline in seeking food instinct. What is more, warmblood horses are often neophobic while non warmblood horse do not show this behavior (Lindberg et al., 1999; Ahrendt et al., 2014). In Valenchon et al. (2013) pilot study it was observed that horses' motivation decreased if exposed too soon after a long delay in receiving food reward. Similar observations were made by Ahrendt et al. (2012). Motivation to work decreased if horses failed to access food during one minute (food worked as a reward in this situation). It is suggested that feral horses do not waste energy to look for food when the risk of failure is high. The incentive value of the stimuli influences horses' performance. When the reward is more attractive, the horses are more motivated and work harder to get it (Lansade et al., 2013). Ninomiya et al. (2007) showed that if the reward is changed from hay to pelleted food, horses operant responses increase and if it is switched from pelleted food to hay, the responses decrease. This result suggests that the rewarding value of the stimuli is of great importance. It is in accordance with research done on rats in a maze. The rat runs faster if it likes food or the amount of food is higher (McClelland, 1987).

It is believed that animals expect the same outcome when they repeat specific behavior. The conflict between expected and received result evokes emotions. In rodents it was observed that if the expectation is not met the hypothalamic-pituitary-adrenal axis is activated and animals show behavior considered as frustration (Berridge, 2001). Animal welfare can be evaluated in context of meeting expectations and frustration indicates its decreasing level (Berridge, 2001). Additionally, frustration may have negative impacts on performance. For example, if the reward is changed from high to low valued, rats slow down the run, likewise animals that received smaller rewards from the beginning maintained constant speed (Toates, 2004). The research on extinction in horses showed that the reward withdrawal caused change in the behavior. Horses exhibited several behaviors that indicated their expectations of the outcome were not met. Some individuals showed repetitive response of learned behavior, others looked into the bowl again and again, or pushed/bit the bowl and the target. It is believed that those behaviors were signs of frustration (Williams et al., 2004).

Conclusions

Understanding learning, motivation and stress mechanisms in the horse are crucial to maintain high levels of welfare and efficient training within the horse management. Horses' performance depends on various characteristics such as breed, temperament, fearfulness, motivation etc. and these influences on horses' behavior cannot be discussed separately. Huge amounts of studies have investigated horses' learning abilities under different conditions and thereby highlighting new areas that still require research. Still it is not known if food motivation correlates with learning abilities or if food can be used to overshadow a stimulus that is known to cause fear reaction.

References

- A arts H., Dijksterhuis A., de Vries P. (2001). On the psychology of drinking: being thirsty and perceptually ready. Brit. J. Psychol., 92: 631–642.
- A d a m c z y k K., G ó r e c k a B r u z d a A., N o w i c k i J., G u m u ł k a M., M o l i k E., S c h w a r z T., E a r l e y B., K l o c e k C. (2015). Perception of environment in farm animals – a review. Ann. Anim. Sci., 15: 565–589.
- A h r e n d t L.P., C h r i s t e n s e n J.W., L a d e w i g J. (2012). The ability of horses to learn an instrumental task through social observation. Appl. Anim Behav. Sci., 139: 105–113.
- Ahrendt L.P., Labouriau R., Malmkvist J.N., Christine J., Christensen J.W. (2015). Development of a standard test to assess negative reinforcement learning in horses. Appl. Anim Behav. Sci., 169: 38–42.
- Berridge K.C. (2001). Reward learning: Reinforcement, Incentives and Expectations, Medin D.L. (ed.). Psychol. Learn. Motiv., 40: 223–278.
- Broom D.M., Fraser A.F. (2007). Domestic animal behaviour and welfare 4th edition. CAB International, pp. 27–51.
- B u c h a n a n T.W., Tranel D., A d o l p h s R. (2006). Impaired memory retrieval correlates with individual differences in cortisol response but not autonomic response. Learn. Memory, 13: 382–387.
- Cahill L., Gorski L., Le K. (2003). Enhanced human memory consolidation with post-learning stress: Interaction with the degree of arousal at encoding. Learn. Memory, 10: 270–274.
- C a l a b r e s e E.J. (2008). Stress biology and hormesis: the Yerkes-Dodson law in psychology a special case of the hormesis dose response. Crit. Rev. Toxicol., 38: 453–462.
- Christensen J.W. (2013). Object habituation in horses: the effect of voluntary versus negatively reinforced approach to frightening stimuli. Equine Vet. J., 45: 298–301.
- Christensen J.W., Zharkikh T., Chovaux E. (2011). Object recognition and generalisation during habituation in horses. Appl. Anim Behav. Sci., 129: 83–91.
- 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.
- Elzinga B.M., Bakker A., Bremner J.D. (2005). Stress-induced cortisol elevations are associated with impaired delayed, but not immediate recall. Psychiat. Res., 134: 211–223.
- Flagel S.B., Robinson T.E., Clark J.J., Clinton S.M., Watson S.J., Seeman P., Akil H. (2010). An animal model of genetic vulnerability to behavioral disinhibition and responsiveness to reward-related cues: implications for addiction. Neuropsychopharmacol., 35: 388–400.
- Freymond S.B., Briefer E.F., Zollinger A., Gindrat-von Allmen Y., Wyss C., Bachmann I. (2014). Behaviour of horses in a judgment bias test associated with positive or negative reinforcement. Appl. Anim. Behav. Sci., 158: 34–45.
- G o o d w i n D. (1999). The importance of ethology in understanding the behaviour of the horse. Equine Vet. J. Suppl., 28: 15–19.

- G o u g h M.R. (1999). A note on the use of behavioural modification to aid clipping ponies. Appl. Anim. Behav. Sci., 63: 171–175.
- Hausberger M., Gautier E., Jego P., Mu C. (2007). Lower learning abilities in stereotypic horses. App. Anim. Behav., 107: 299–306.
- H a w s o n L.A., M c L e a n A.N., M c G r e e v y P.D. (2010). The roles of equine ethology and applied learning theory in horse-related human injuries. J. Vet. Behav., 5: 324–338.
- Held S., Cooper J.J., Mendl M.T. (2009). Advances in the Study of Cognition, Behavioural Priorities and Emotions. The Welfare of Pigs. Springer Netherlands, pp. 47–94.
- H e n d r i k s e n P., E l m g r e e n K., L a d e w i g J. (2011). Trailer-loading of horses: Is there a difference between positive and negative reinforcement concerning effectiveness and stress-related signs? J. Vet. Behavior., 6: 261–266.
- Hori Y., Ozaki T., Yamada Y., Tozaki T., Kim H.-S., Takimoto A., Fujita K. (2013). Breed differences in dopamine receptor D4 gene (DRD4) in horses. J. Equine Sci., 24: 31–36.
- Janczarek I., Stachurska A., Wilk I. (2014). Which horses are most susceptible to the initial natural training? Ann. Anim. Sci., 14: 637–648.
- Joëls M., Pu Z., Wiegert O., Oitzl M.S., Krugers H.J. (2006). Learning under stress: How does it work? Trends Cogn. Sci., 10: 152–158.
- Lansade L., Simon F. (2010). Horses' learning performances are under the influence of several temperamental dimensions. Appl. Anim Behav. Sci., 125: 30–37.
- 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. Proc., 91: 94–102.
- Lansade L., Coutureau E., Marchand A., Baranger G., Valenchon M., Calandreau L. (2013). Dimensions of temperament modulate cue-controlled behavior: a study on Pavlovian to instrumental transfer in horses (*Equus caballus*). PloS One, 8(6), 64853.
- L e i n e r L., F e n d t M. (2011). Behavioural fear and heart rate responses of horses after exposure to novel objects: Effects of habituation. Appl. Anim Behav. Sci., 131: 104–109.
- Lindberg A., Kelland A., Nicol C. (1999). Effects of observational learning on acquisition of an operant response in horses. Appl. Anim Behav. Sci., 61: 187–199.
- Lorenz K. (1966). On Aggression. Methuen, London.
- M a r t i n T.I., Z e n t a 11 T.R., L a w r e n c e 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.
- M c C a 11 C.A. (1990). A review of learning behavior in horses and its application in horse training. J. Anim. Sci., 68: 75–81.
- M c C l e l l a n d D.C. (1988). Human motivation. New York: Cambridge University Press, p. 4, 84, 553.
- M c G r e e v y P. (2004). Equine behaviour. A guide for veterinarians and equine scientists. Saunders, Elsevier Ltd., 369 pp.
- McGreevy P., McLean A. (2010). Equitation Science. Wiley-Blackwell.
- M c L e a n A.N. (2008). Overshadowing: a silver lining to a dark cloud in horse training. J. Appl. Anim. Welf. Sci., 11: 236–248.
- M e n d l M. (1999). Performing under pressure: stress and cognitive function. Appl. Anim Behav. Sci., 65: 221–244.
- 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. Proc., 106: 141–150.
- M ills D.S. (1998). Personality and individual differences in the horse, their significance, use and measurement. Equine Vet. J. Suppl, 27: 10–13.
- Mills D.S., Marchant-Forde J.N., McGreevy P.D., Morton D.B., Nicol C.J., Phillips C.J.C., Sandøe P., Swaisgood R.R. (2010). The Encyclopedia of Applied Animal Behaviour and Welfare. CAB International, UK, pp. 124–125, 512–513.
- M u r p h y J., H a 11 C., A r k i n s S. (2009). What horses and humans see: a comparative review. Int. J. Zool., ID 721798: 1–14.
- N i c o l C. (2002). Equine learning: progress and suggestions for future research. Appl. Anim Behav. Sci., 78: 193–208.
- Nicol C.J. (2006). How animals learn from each other. Appl. Anim. Behav. Sci., 100: 58-63.

- Ninomiya S., Mitsumasu T., Aoyama M., Kusunose R. (2007). A note on the effect of a palatable food reward on operant conditioning in horses. Appl. Anim Behav. Sci., 108: 342–347.
- R o b i n s o n T.E., F l a g e l S.B. (2009). Dissociating the predictive and incentive motivational properties of reward-related cues through the study of individual differences. Biol. Psychiat., 65: 869–873.
- R o o z e n d a a 1 B. (2000). Glucocorticoids and the regulation of memory consolidation. Psychoneuroendocrinol., 25: 213–238.
- R o o z e n d a a 1 B. (2002). Stress and memory: opposing effects of glucocorticoids on memory consolidation and memory retrieval. Neurobiol. Learn. Mem., 78: 578–595.
- 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.
- Rothman J., Christensen O., Søndergaard E., Ladewig J. (2014). Behaviour observation during conformation evaluation at a field for Danish Warmblood horses and associations with rideability and performance traits. Equine Vet. J., 34: 288–293.
- S and i C., P in elo-N ava M.T. (2007). Stress and memory: behavioral effects and neurobiological mechanisms. Neural Plast., 2007: 1–20.
- Schmidt A., Möstl E., Wehnert C., Aurich J., Müller J., Aurich C. (2010). Cortisol release and heart rate variability in horses during road transport. Horm. Behav., 57: 209–215.
- Schwabe L., Wolf O.T. (2010). Learning under stress impairs memory formation. Neurobiol. Learn. Mem., 93: 183–188.
- S c h w a b e L., B o h r i n g e r A., C h a t t e r j e e M., S c h a c h i n g e r H. (2008). Effects of prelearning stress on memory for neutral, positive and negative words: Different roles of cortisol and autonomic arousal. Neurobiol. Learn. Mem., 90: 44–53.
- Schwabe L., Joëls M., Roozendaal B., Wolf O.T., Oitzl M.S. (2012). Stress effects on memory: An update and integration. Neurosci. Biobehav. R, 36: 1740–1749.
- To a t e s F. (2004). Cognition, motivation, emotion and action: a dynamic and vulnerable interdependence. Appl. Anim Behav. Sci., 86: 173–204.
- Valenchon M., Lévy F., Fortin M., Leterrier C., Lansade L. (2013 a). Stress and temperament affect working memory performance for disappearing food in horses, *Equus caballus*. Anim. Behav., 86: 1233–1240.
- Valenchon M., Lévy F., Górecka-Bruzda A., Calandreau L., Lansade L. (2013 b). Characterization of long-term memory, resistance to extinction, and influence of temperament during two instrumental tasks in horses. Animal Cognition, 16: 1001–1006.
- Valenchon M., Lévy F., Prunier A., Moussu C., Calandreau L., Lansade L. (2013 c). Stress modulates instrumental learning performances in horses (*Equus caballus*) in interaction with temperament. PloS One, 8(4), e62324.
- Visser E., van Reenen C., Schilder M.B., Barneveld A., Blokhuis H. (2003). Learning performances in young horses using two different learning tests. Appl. Anim Behav. Sci., 80: 311–326.
- Von Lewinski M., Biau S., Erber R., Ille N., Aurich J., Faure J.-M., Aurich C. (2013). Cortisol release, heart rate and heart rate variability in the horse and its rider: different responses to training and performance. Vet. J., 197: 229–232.
- Wang X., Sánchez B.N., Golden S.H., Shrager S., Kirschbaum C., Karlamangla A.S., Diez Roux A.V. (2014). Stability and predictors of change in salivary cortisol measures over six years: MESA. Psychoneuroendocrinol., 49C: 310–320.
- Williams J.L., Friend T.H., Nevill C.H., Archer G. (2004). The efficacy of a secondary reinforcer (clicker) during acquisition and extinction of an operant task in horses. Appl. Anim. Behav. Sci., 88: 331–341.
- Wolff A., Hausberg er M. (1996). Learning and memorisation of two different tasks in horses: the effects of age, sex and sire. Appl. Anim. Behav. Sci., 40: 137–143.

Received: 10 VII 2015 Accepted: 12 I 2016