Genetics Of Horse-Human Interactions

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Domestication and History of Horse-Human Interactions

Horses have been part of the human culture for more than 15,000 years (Goodwin, 1999), and it is estimated that the onset of their domestication dates back to approximately 3000 BC (Outram et al, 2009). Other authors suggest dates as early as 5000 BC (e.g. Levine, 1999; Price, 2002). Since there is little direct evidence revealing exact stages of horse domestication, the beginning date is a contentious issue (c.p. Levine, 2005). Anthony and Brown (1991) found archaeological evidence of riding that dates back to approximately 4000 BC, indicating either that horses were employed for riding before they were domesticated or that domestication may indeed have started earlier than 3000 BC. In the process of domestication, human beings likely actively selected the more docile individuals for husbandry and breeding (Hediger, 1938; Price, 1984). Traits related to fear can be changed over relatively short periods of time by intentionally (Reese, 1979; Plomin, 1990) or unintentionally (Hearnshaw and Morris, 1984; Boissy et al., 2005) genetically selecting either fearful or calm individuals. There is evidence that, indeed, selection for tameness is the driving force in domestication (Trut et al., 2004). Yet, domestication generally changed behaviour only quantitatively by modifying stimulus thresholds and not qualitatively (Jensen, 2002). Accordingly, all types of behaviour typical for the wild ancestors are still present to some degree in the domesticated individuals of that species. Also, horses have been naturally and artificially selected for the great majority of their evolutionary time for physical characteristics such as speed, strength and agility, which enable them to survive in the wild or to perform their designated work. However, with the possible exception of some recent attempts, they have not been bred for the role as a companion animal. Consequently, traits of the behavioural repertoire - other than fearfulness towards human beings - probably changed little over the process of domestication (Goodwin, 1999). Regardless of the exact timing and location of domestication, horseback riding has brought about substantial cultural and economic shifts (Anthony and Brown, 1991). Horses have become a significant economic sector of the animal industries (e.g. Corbally et al., 1999). Originally used with the purpose of transportation and warfare (Levine, 1999), today, riding in the Western world is mostly undertaken as sport or recreational activity. Nevertheless, the popular equitation styles and riding theories nevertheless originate from working conditions such as farm work (Western riding) or military purposes (English riding) typical to particular regions and eras. Still, today, the disciplines of dressage and show-jumping are the two most popular equestrian sport disciplines (cp. Koenen et al., 2004), both with leisure and competition riders up to Olympic level (FEI, 2007).

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The role of the different senses in the human-horse communication

Communication between human beings and horses is a key factor in all human-horse interactions. Several studies showed that human beings can have both positive (Lynch et al., 1974; Feh and de Mazières, 1993; McGee and Smith, 2004) and negative (Henry et al., 2005) effects on emotional states of the horse, depending on the type and quality of the interaction. Moreover, Hausberger and Muller (2002) showed that horses can also generalize their experience with humans, such that their previous experience with their caretaker carries over to reactions to strangers. Communication between the two species can ensue consciously or subconsciously (von Borstel, 2009) via visual, tactile, auditory, olfactory and – using communication in a broad sense - also via gustatory signals. Horses' reactions to similar stimuli within one sense are reasonably stable across time and situations (Lansade et al., 2008) to classify them as components of temperament. However, while research on horse-human communication is scarce, even less is known about the extent and means of the subconscious communication that accompanies, and often overrides, the conscious communication from human beings to horses.

Tactile communication. Communication via tactile stimuli is the predominant method of interaction between rider and horse during riding. Traditional horse training almost exclusively relies on negative reinforcement: The rider applies varying degrees and patterns of tactile pressure with his bodyweight, legs and hands on the horse's back, flanks or mouth, respectively, which is released when the horse gives the desired response. In many cases the rider's actions are amplified by spurs, a whip and/or a curb, i.e. a bit with leverage effect. However, horses are very sensitive to tactile stimuli (Saslow, 2002), and horses are skilled at generalizing from trained tactile stimuli to similar stimuli varied in intensity and/or location (Dougherty and Lewis, 1993). Therefore, subtle signals can be very effective in horse training. A stronger emphasis on subtle cues when training the horse for riding could improve the riding horses' welfare (Ödberg and Bouissou, 1999). The horse's innate tactile sensitivity can be expected to contribute significantly to its trainability and rideability. Likely an optimum degree of tactile sensitivity exists. Neither overly sensitive horses that readily experience pain at larger intensities of tactile stimulation, nor excessively insensitive horses that require forceful tactile stimulations would be desirable in riding. Tactile sensitivity may be linked to fearfulness, such that horses that reacted less to a fine tactile stimulation at the withers may be less fearful, whereas horses that were more sensitive also showed stronger fear reactions (Lansade et al.,). In general, horses are able to discriminate finer differences in tactile stimuli than human beings can (Saslow, 2002). Horses may even be able to detect changes in its rider's emotional state based on changes in rider's muscle tension that result in slightly different patterns of tactile stimulation by the rider. In a series of experiments (summarised in von Borstel, 2009), I showed that horses reacted differently to riders who were truly nervous (von Borstel et al., 2005) and those who pretended to be nervous (von Borstel and König, 2008). Although communication via other senses could not be entirely excluded, the tactile cues seems the predominant stimulus to which the horses reacted.

Visual communication. As a flight animal that evolved in the open grassland, horses heavily rely on vision for both predator detection (Saslow, 2002) and communication with each other. Consequently, horses have a highly developed visual system with a approximately 320 degrees field of view (McGreevy, 2004). Even if horses don not have great acuity in vision (Saslow, 2002), they see particularly well at night (Hanggi and Ingversoll, 2004) and are able to distinguish a number of colours (Macuda and Timney, 1999). Perhaps as a result of their well developed vision and intraspecies visual communication system, visual signals seems to be their first choice, both for conveying information to people (e.g. using threatening mimic and gestures towards human beings) and for obtaining information from a human handler on the ground. As famously revealed by Pfungst's (1983) observations, the horse Clever Hans used visual signals unintentionally given by his owner, rather than relying on the auditory signals, i.e. words, that the owner spoke with the intention of communicating with Clever Hans. Practical experience and anecdotal evidence also suggests that horses predominantly pick up intentionally and/or unintentionally given visual signals during longeing instead of reacting to the auditory cues given by the handler. Animals' ability to correctly interpret human gestures without prior training has been suggested to be a trait shaped by domestication. Hare et al. (2002) showed that adult as well as juvenile dogs, but not naturally or hand-raised wolves were able to correctly interpret human pointing gestures. Another group of researchers (McKinely and Sambrook, 2000) compared dogs and horses with regard to this ability, and found that horses, unlike the dogs, were unable to use the pointing cues to locate feed. However, the number (n=4) and choice of horses was suboptimal, raising concerns about the overall validity of these findings. The two breeds Thoroughbred (n=2) and Anglo-Arab (n=1) of the three breeds they (McKinely and Sambrook, 2000) had chosen for their experiment are known to perform poorer than all other tested breeds in learning tasks (Hausberger et al., 2004), with Welsh ponies (the 4th subject in McKinely and Sambrooks study) showing average learning performance. In fact, the only horse that did perform well in the pointing task of McKinley and Sambrook's (2000) experiment was the Welsh pony, while the Thoroughbreds did not use the experimenter's pointing cues to find the food. These differences may in part be due to breed differences in excitability. However, they may also be due to the Welsh ponies being more intensively selected for components of horse-human interactions, rather than primarily for athletic performance. An exhaustive comparison between breeds of horses would aid to assess the validity of the assumption that the more domesticated breeds of horses are better at interpreting human gestures. In addition, the degree of familiarity between research subjects and testing person may be a confounding factor of the experiment, as the dogs were tested by their owners, but the horses by the experimenter. Research on neuron activity shows that sheep perceive humans as predators rather than conspecifics unless the humans were familiar to them and associated with feeding (Kendrick, 1991). This may apply similarly to horses which are prey animals, too, thus inhibiting learning performance.

Auditory communication. Horses' optimum hearing ranges between 1 and 16 kHz, but their hearing range extends from 55 Hz to 33.5 kHz, which is considerably higher than that upper threshold for human beings (Heffner and Heffner, 1983). Horses attend to auditory and non-auditory stimuli by pointing their ears in the direction of the stimulus, indicating that hearing is a very important sense to horses. Vocalisations in horses include screams, squeals, nickers, whinnies, snorts, and blows (Browning and Scheifele, 2004), all of which are assumed to have specific communicative values. However, most vocalisations are used in emergency situations (e.g. whinnies of horses and alarm snorts) and in general, horses do not vocalize very frequently. People, on the other hand primarily rely on language, i.e. auditory communication, in order to communicate with each other. This habit is extrapolated to communication with other species, such as horses. Although the human voice lies well within the hearing range of horses (Saslow, 2002), it may not their first choice of extracting information from human signals (see chapter on visual communication). A potential explanation may be that it is difficult for human beings to hide their emotions in their voice. Thus vocal signals may vary depending on the handler's mood (Saslow, 2002), and as a result lack the consistency required for efficient learning in horses. Nevertheless, horses are well able to learn auditory cues (see e.g. Williams et al., 2004), and while they are at most an asset during riding and ground work, they are a central means of communication during driving, when visual communication is prevented by blinkers and tactile communication limited to rein and whip cues.

Chemoreception: olfactory communication. Perhaps owing to the relatively poorly developed, and thus less important, olfactory sense in humans, little attention is paid to olfaction in horses. Evidently, olfaction is an important means of intraspecific communication in horses. For example, when two unfamiliar horses meet, they almost invariably meet nose to nose (McGreevey, 2004), apparently in order to exchange information about each other through smell. Also, an important means by which stallions detect whether a pile of dung stems from a male rival or a female harem-member (Stahlbaum and Houpt, 1989) or by which they monitor the mares' cycle (Lindsay and Burton, 1983) is the olfactory testing of dung or urine, respectively. In mare-foal recognition olfaction also appears to be an important factor (Wolski et al., 1980). With regard to horse-human communication, it could be speculated that horses can gain important information from humans' body secretions. In a manner similar to interaction with other horses, horses nose at people when given the opportunity (c.p. e.g. Lansade et al., 2008). Emotional states such as fear, anxiety and anger are likely to be conveyed through volatile or non-volatile substances like pheromones. Although the existence of pheromone communication among human beings still is controversially discussed (Wysocki and Petri, 2004), there is evidence that humans exude different odours depending on their emotional states. For example, Ackerl et al. (2002) showed that in an experimental setting, women could distinguish smells from fearful and non-fearful human beings. In practice, however, this means of communication likely remains imperceptible, or at least subconscious, to human beings, which may have important implications for horse-human interactions: Even a person who is able to control their actions to an extent that their posture and gestures do not convey information about their true emotional state, could not hide their emotions entirely from the horse. Possibly, the communication of nervousness from rider to horse (von Borstel et al., 2009) can in part also be attributed to olfactory communication.

Chemoreception: gustatory communication. Olfactory and gustatory senses are closely linked in the horse (Lansade et al., 2008), and horses are able to differentiate between a variety of tastes (Goodwin, 2005). In a broad sense, gustatory communication from human to horse is possible and gains popularity with the rise of more sympathetic training methods: Feeding titbits directly as a reward or by combining feed with a secondary reinforcer (e.g. Williams, et al., 2004) that then can be used in training independent from the actual feed rewards acts directly or indirectly through the gustatory sense on the horse. As such, the communication via the gustatory sense is a very powerful tool in horse training. Indeed, research suggests, that training via rewards may yield better and/or faster results than the traditional training techniques using negative reinforcement (Innes and McBride, 2008; Sankey et al., in press). Several studies found individual differences in learning (e.g. Fiske and Potter, 1979; Heird et al., 1986), and the authors attribute these to differences in ease of distractedness and emotionality. Not much is known about genetic differences in trainability using rewards, however, breed differences are evident (Lindberg et al., 1999), and it is suggested that generally more cold-blooded breeds of horses and ponies that have evolved under harsh conditions may be more motivated by a nutritional reward than warm-blooded horses, including Arabs and Thoroughbreds. When applied correctly, positive reinforcement using feed rewards may improve horse training, since it is a form of communication easily understood by the horse. Detailed analyses of the physiological and genetic background of individual differences are yet to be conducted.

Genetic evaluation of traits related to horse-human interactions

Traits evaluated in performance tests. Given the popularity of dressage and show-jumping, it is not surprising that in Europe a substantial number of sport horse breeding associations (Koenen et al., 2004) conduct sophisticated performance tests and subsequent breeding value estimation for traits relevant to the these disciplines. Recently, the US also adopted a performance test for warmblood riding horses (Könnel, 2009). Icelandic horses are one of the rare exceptions in which an across-country breeding value estimation is conducted, and for traits relevant to disciplines outside the English riding style, i.e. the special gaits tölt and pace (Árnason, 1984) that are specific to only a few breeds of horses. Generally, traits that are evaluated include conformation characteristics (e.g. size, proportions, correctness of extremities and back, etc), the gaits (walk, trot, gallop) and jumping ability, health traits, as well as personality traits (e.g. temperament, character, handling ease, willingness to work, rideability). These traits are evaluated either in hand or under the rider. Only in a few cases evaluation takes place when the horse is running freely (e.g. free-jumping). Nevertheless it takes place in the presence of people that directly or indirectly influence the horse. Therefore, all traits are directly or indirectly dependent on and influenced by the quality of horse-human interactions.

Examples of people's influence on equine performance traits. For instance, a horse that is fearful of people may be more distracted by the spectators and thus show poorer performance during free-jumping. This influence may even apply to a lesser degree to health and conformation traits, because their evaluation can be slightly influenced by the way the horse is positioned in front of the judges, although these effects are generally considered to be negligible. In contrast, the gaits are under considerable influence from both the rider (c.p. Peham et al., 2004) or handler. For example, a less skilled rider or an unathletic handler may hinder the horse's movements, thus not allowing it to express its true performance potential. For that reason, competition data are corrected for the effect of the individual rider or her/his skill level (von Velsen-Zerweck, 1998). Nevertheless, heritabilities for traits assessed during competition are significantly lower than heritabilities for the same traits assessed during performance tests on station (von Velsen-Zerweck, 1998), indicating that there are numerous environmental factors influencing the horse's performance. Most evident, however, is the handler's and rider's influence on the horse's personality traits. Indeed, the traits "character" and "handling ease" aim to evaluate the horse's interaction with human handlers, which, however, is highly trainable. Houpt and Kusunose (2001) found no breed differences in a survey regarding trailer-loading problems, a highly training-dependent handling procedure. The other personality traits such as temperament and rideability are also the result of a complex interaction between horse and handler. For example a horse may have the genetic basis for expressing strong fear reactions, but if it is also very fearful of the rider's punishment in response to shying, it may not fully express these strong fear reactions when ridden. Fear reactivity and anxiety in handling situations, which are important components of temperament, differ considerably between breeds (Hausberger et al., 2004), and sire effects (Wolff et al., 1997), as well line effects have been found: horses with high genetic merit for show-jumping reacted less strong than horses with high genetic merit for dressage or horses with average genetic merit in either disciplines, regardless of whether or not horses were trained in their discipline (von Borstel et al., submitted). However, fear reactions, are also highly influenced by training (e.g. Christensen, 2006), the present riding style (von Borstel et al., 2009) and previous experience, including that with human beings (Jezierski et al., 1999). We compared horse's reactions to the same temperament test when ridden, led, and running freely, and phenotypic correlations for traits such as activity, reactivity and emotionality ranged between non-significance (activity in ridden and free-running tests) and 0.66 (reactivity in ridden and led tests) (Euent, 2009, König von Borstel et al., submitted). These values indicate a considerable influence of the human handler and rider on the horse's behaviour at the phenotypic level, but also a horse-specific, unaltered component. At present, very little is known about the interaction of environmental and genetic factors with regard to these personality traits. Indirectly, the genetic aspect of horse-human interactions can be evaluated by examining the genetic correlations between the same trait evaluated in performance tests under the rider and in hand and/or free-running. In general these genetic correlations between the same traits evaluated during different situations are high, ranging between 0.68 (overall dressage performance in mare performance test and competitions; Brockmann, 1998) to 0.98 (free-jumping and jumping under rider, Brockmann, 1998) but amount only in a few cases to 1.0 (gaits in stallion performance tests and riding horse quality tests, Gerber Olsson et al., 2000). The fact that the genetic correlations are commonly imperfect indicates that there are small discrepancies in the genes determining performance in the same trait assessed in the different testing situations. This consideration provides evidence of a genetic basis for the horse's reaction to human handling. In other words, the way a horse responds to a rider is governed by slightly different genes than the way the horse response to a handler, which is yet different to the horse's behaviour without the influence of a human rider or handler. On the other hand, small differences in genetic values should not be over-interpreted, since evaluation of performance, and particularly the personality traits, in horse breeding is flawed for a number of reasons: Horses are pre-selected, grades are often assigned subjectively rather than using objective criteria, the scale of grades is not sufficiently utilized, resulting in non-normally distributed scores with high means and very low standard deviations (Pirsich et al., 2009). All of the above factors violate the assumptions of the statistical models used in breeding value estimation, thus leading to bias in the values and potentially distortion of the results.

Longevity. Owing to the lack of available information, consideration of longevity in genetic evaluation of horses is a largely neglected area. This is unfortunate, since the horses' longevity is a key measurement of overall time people spend interacting with their horses. Unlike with other livestock species kept for economic purposes, culling in horses is a multidimensional issue, depending very much on the horse's present owner and her/his financial situation as well as her/his emotional attachment (see e.g. Keaveney, 2007) to the animal. Sport horses may be culled for poor health (which commonly results from poor husbandry conditions; von Borell, 2002) or insufficient performance; However, most often they will be kept by the owner or sold to less ambitious riders regardless of poor performance, due to the emotional value the owner or future owner attaches to the horse. However, longevity defined as the length in time, a horse competes in sport may be a measure for the horses' suitability for a particular discipline. Friedrich (2010) found breed differences in longevity of dressage horses. Thoroughbreds were used on average 3 years, while Hanoverians were used 5 years in competitions, which can likely be attributed to differences in genetic ability for dressage. Even if the human handling is the most important factor in determining the quality of horse-human interactions, genetic selection for longevity in horses would likely improve horses' interactions with human beings on the genetic level, since horses interacting with people in a desired manner are much more likely to be kept for a longer time, than horses showing undesired interaction traits.

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