Understanding the perceptual world of horses

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Abstract

From the viewpoint of experimental psychology, there are two problems with our current knowledge of equine perception. The first is that the behavioral and neurophysiological research in this area has enormous gaps, reflecting that this animal is not a convenient laboratory subject. The second is that the horse, having been a close companion to humans for many millennia, entrenched anecdotal wisdom is often hard to separate from scientific fact. Therefore, any summary at present of equine perception has to be provisional. The horse appears to have developed a visual system particularly sensitive to dim light and movement, it may or may not have a weak form of color vision in part of the retina, it has little binocular overlap, and its best acuity is limited to a restricted horizontal band which is aimed primarily by head/neck movements. However, the total field of view is very large. Overall, as would be expected for a prey animal, horse vision appears to have evolved more for detection of predator approach from any angle than for accurate visual identification of stationary objects, especially those seen at a distance. It is likely that, as for most mammals except the primates, horses rely more heavily on their other senses for forming a view of their world. Equine high-frequency hearing extends far above that of humans, but horses may be less able to localize the point of origin of brief sounds. The horse's capacity for chemoreception and its reliance on chemical information for identification may more closely resemble that of the dog than of the human. Its tactile sensitivity is high, and the ability of its brain and body to regulate pain perception appears to be similar to that found in other mammals. There is room for a great deal of future research in both the area of equine perception and sensory-based cognition, but for the present time persons interacting with this animal should be made aware of the importance of the sounds they make, the movements of their bodies, the way they touch the animal, and the odors they emit or carry on their clothing.
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1. Introduction

I am glad that I did not have occasion to look at the histology of the horse eye until long after I had stopped riding horses at speed over large jumps. Like most riders, my naive assumption was that horses saw what I saw. However, given the construction of its retina (the light sensitive layer of an eye) the horse cannot possibly have the human's daytime capacity to resolve detailed images or recognize objects by vision alone (Hebel, 1976). It was sobering to realize the extent to which the safety of both of us had been dependent on my eyes and my riding skills.

2. The useful concept of "Umwelt"

Once, we humans had devised ways to measure the physical world, it became apparent that our perception of "reality" was a construction of our human minds and not a faithful physical replica (Plato, in Russell, 1945). Our sensors function as filters which pass only a minute proportion of physical energies. Our brain uses this fragmentary information to construct a view of the world that was advantageous to the survival of our primate ancestors. There is no "color" in light. A "sound" does not occur unless it is in a frequency range that can be heard. The same object pressed against our skin may variously produce perceptions of "heat", "cold", "pain", "vibration", "tickle", "touch", etc., depending on the location and circumstances of contact. Many things that have tastes or smells to us in our teens evoke little or no sensation in our seventies (Schiffman, 1977; Schiffman and Pasternak, 1979).

Within the human species, there is generally a high level of agreement of perceptions, although age, gender and, especially, nervous system damage (Grandin, 1995; Sacks, 1985), can yield discrepancies. However, the difference between species is great both in the sensory information that is available and the particular interpretation made of that information by the brain. Early in the 20th century, J. von Uexkull (Drickamer et al., 1996) used the term "Umwelt" to characterize the particular perceptual world of a species. Each species evolves the Umwelt which allows it to extract from the external world the information its ancestors needed for survival.

It is difficult to shake off one's own species-specific perception of reality (Brown and Deffenbacher, 1979). When we interpret the actions of our companion animals, we are prone to attribute behavioral shortcomings or peculiarities to "lack of intelligence" and "deficient obedience" on the one hand or to animal extrasensory perception ("ESP") on the other. But often the best explanation is a mismatch of Umwelts.

3. Psychophysical sources of information about a foreign Umwelt

Gaining reliable information about the relationship between physical stimulation and perceptual response is not easy, even from human subjects with whom researchers share Umwelt and language. Persons working in this area must first thoroughly understand the physics of stimulation. For example, in color vision research, it is important to know that colored paints do not provide single-wavelength stimulation of the eye and in research on

hearing, it is necessary to understand that only by use of headphones or an anechoic testing booth can the researcher be certain that the stimulus produced by the researcher is exactly the same as the stimulus that reaches the eardrum.

It is just as difficult when doing psychophysics to devise measures of behavior that reveal underlying sensations and perceptions. Psychologists have spent a century and a half devising reliable and valid methods for use with adult human subjects. Adaptation of these techniques for use with non-language subjects, such as human infants and animals, is difficult (Penner, 1995; Stebbins, 1970). Reliable and valid experiments with animal subjects are likely to be very lengthy. It took 7 months of two-choice discrimination training, for example, for Entsu et al. (1992) to measure daytime visual acuity in three cows and several months for Scott and Milligan (1970) to train two monkeys to the point where they could measure the extent of the visual spiral aftereffect, a visual illusion of contraction or expansion of stationary objects experienced by humans.

Even doing human psychophysics traditionally requires hundreds of trials per subject and, therefore, we try to get by with small samples. However, it is accepted in small-sample human psychophysics that all normal individuals must show results in close agreement or the methodology is suspect. Psychophysical information from small-sample animal studies which report one kind of results for one or two animals and a different result for a third can be hard to interpret. Animal psychophysics is a field for researchers who are patient and do not require quick answers.

4. Neurophysiological and neuroanatomical sources of information

Psychophysicists have traditionally relied on data from neurophysiology and neuropsychology to suggest experiments and confirm behavioral results. If we have detailed histological information on the structure of an animal's sensory systems, especially if it is backed up with electrophysiological recording, then often we can dispense with more laborious behavioral investigations. Jacobs' (1981) conclusions about the existence of color vision in dogs, for example, are solidly based on both behavioral and electrophysiological observations.

Unfortunately, large, expensive, unwieldy horses are not ideal laboratory animals for histological or neurophysiological research. Thus, there is limited information from these biological indicators of perceptual capacities. For example, reliable counts of cone and rod photoreceptor distributions at different locations of the horse retina would go a long way to resolving issues about acuity, movement sensitivity, depth perception, and possible color vision. However, as of now, researchers interested in equine vision still must base their arguments on next-stage ganglion cell densities obtained by Hebel in 1976 (Harman et al., 1999; Timney and Keil, 1992; Saslow, 1999).

5. Comparative sources of information

Perceptual mechanisms tend to be conservative in evolution. Therefore, information from related species often is valuable. Our understanding of the Umwelt of other primates

has been greatly helped by the similarity of their perceptual equipment to our own. However, as we try to understand mammals with very different evolutionary histories and very different survival strategies, such generalizations weaken. Since primates evolved in an arboreal world amidst heavy vegetation, it is very unlikely that they have the same perceptual capacities as a ground animal who evolved in open habitat. Since our own hominid line of primates adopted a partially predator lifestyle, it is more likely that our Umwelt will show more correspondence with those of our predatory companion animals, such as the dog or cat, than with prey species like horses or cattle. Thus, we must be particularly cautious when generalizing human perceptions to our horse companions.

6. Ethological sources of information

Another way to guess about species differences in perceptual capacities is to look at the role that a particular kind of sensory information plays in a species' adaptation to its environment. Unfortunately, since vision looms very large in a primate's relationship to its physical world, human investigators have tended to overemphasize the importance of vision for other animals. Since we humans rely heavily on our excellent high-acuity daytime vision for distance information, object recognition, sexual attraction, kin/friend identification, and non-verbal communication of emotion, we often overlook the fact that most other mammalian species use olfaction or hearing for these purposes. In the scant research literature on horse perception, the bulk of studies have been on vision while senses probably of more crucial importance to the horse Umwelt have been neglected.

7. A very important distance sense: olfaction

The vertebrate cerebral hemispheres developed from the roof of the olfactory lobe. Olfaction was the principal sense that animals coming out on land exploited for ''distance'' information. The limbic system of the mammalian brain, which regulates emotion and motivation, was originally driven primarily by olfactory input. While in primates, and especially humans, olfactory structures have greatly diminished, the horse brain has extremely large olfactory bulbs with a convoluted surface. Since densities of olfactory receptor cells remain constant per unit surface area, the extent of olfactory epithelium determines the total quantity of receptors. The extensive size of the smoothed-out epithelium of the horse olfactory bulb implies that volatile odors should form a much more significant part of their Umwelt than is the case for humans.

The potential for obtaining olfactory information about the physical world is also affected by nasal structure and breathing patterns. The horse nose can move large volumes of air at one breath and trap large numbers of molecules. An additional equine anatomical advantage is that the horse has its nostrils separated and pointed in opposite directions, permitting stereolfaction in localization of olfactory sources (Stoddart, 1980).

Another anatomical indicator of the potentially large role chemosensing plays in forming the equine Umwelt is that the horse has a prominent vomeronasal (Jacobson's) organ, an accessory olfactory structure which is nearly vestigial in humans. While the

epithelium of the olfactory bulbs responds to smaller, volatile molecules, the vomeronasal organ is more responsive to non-volatile, large, species-specific molecules such as are found in body secretions (Coren et al., 1999). Such chemicals are excellent candidates for the role of "pheromones", chemicals which are released by one member of a species and produce automatic hormone-like reactions in another.

Unfortunately, the anatomical likelihood of olfactory perception forming a major part of a horse's Umwelt is not consistent with the small number of published studies on horse olfaction. Most olfactory research has concentrated on the possible role of pheromones in horse mating behavior. If the flehmen response (lip-curling with inhalation which draws substances into the vomeronasal organ) is used as an indicator, then stallions appear to make use of this form of chemical sensitivity more often than mares or geldings (Marinier et al., 1988). However, it is likely that other olfactory routes also play a role in mammalian response to both sexual and non-sexual pheromones (Stoddart, 1980). One study indicated that the flehmen response in unconfined stallions preceded marking rather than copulatory behavior (Stahlbaum and Houpt, 1989).

In my own barns, I have seen vigorous flehmen responses from mares and geldings as well as stallions when the stimuli were secretions connected with birth of a foal rather than the more usual research stimulus of urine from a mare in estrus. Horses also may make flehmens to objectionable odors (one fussy mare consistently makes a flehmen to the smell of dog food on my fingers when I try to feed her from an insufficiently washed hand). Much more research is needed with a greater variety of stimuli using both confined and unconfined horses to ascertain exactly what role this kind of chemical sensitivity plays in domestic horse behavior.

We also need to look for priming effects of pheromones such as have been found in other species. For example, pheromones released by an adult dominant stallion might suppress or retard maturation of hormonal systems in younger males who remain in close social contact as well as stimulate estruos cycles in females. In humans, it appears that a pheromone causes menstruation to synchronize in females who dwell together (McClintock, 1971). In mice, the smell of urine from an unfamiliar male can cause pregnant females to abort (Bruce, 1960). Hines (1997) has referred to these kinds of direct effects as "unconscious odors".

Olfactory stimuli have the advantages of providing information both day and night and of not requiring the originator of the odor to remain present. In one sense, scent marks can provide for animals some of what writing has come to provide for humans. Since horses are not territorial, it is likely they will show less marking behavior than, for example, dogs. However, Miller (1981), in a study of feral horses, found that stallions not only responded to manure piles of other stallions by covering them with their own feces but also responded differentially if the manure had been deposited by a familiar stallion to whom they had previously lost a battle.

There is certainly a need for more research on scent identification, kin recognition, and marking by horses. Whereas humans "recognize" one another when they see a face, horse greetings include standing parallel and sniffing under one another's bellies. When one of my stallions goes out into a commonly shared pen, he ignores his feed until he has sniffed every available pile of manure and marked those made by other males. No similar behavior occurs in mares (who always head straight for the food). If the stallion's companion mare or

her foal drops fresh manure, however, he is likely to urinate on it rather than defecate. In an open-field observational study, we found that the stallions and geldings, who usually roll soon after being turned out individually in an arena covered in sawdust, were not picking their rolling spots at random. They sniff before going down and roll in the same area in which the previous horse had rolled. Possibly, as in some other ungulates, they are trying to build up a certain ''family'' or ''masculine'' scent.

On the trail, we allow our riding horses to drop their heads to see what stimuli they will pursue. From about 4 years of age on, the stallions voluntarily pause for each pile of manure. The subsequent marking sequence can be lengthy, involving intense sniffing and licking. While engaged in this behavior, the horse attends little to rider signals and is willing to let the other horses in the group continue without him. He then either resumes his progress or, if he decides to mark, steps forward, deposits a few lumps of manure, and then turns and resumes entranced sniffing. He may repeat this ritual once or twice more before proceeding. The piles he is most likely to mark with feces are his own or those of other males from our operation. Mares on the trail show little or no interest in manure piles and stallions who are gelded gradually lose this behavior pattern.

The sensitivity of a stallion to a marking site can be impressive. The pile does not have to be fresh to attract his attention. One day, a 6-year-old stallion suddenly stopped, sniffed, turned around and with his nose to the gravel road backtracked a wavering path for about 25 ft. We then saw that the ''trace'' he had been following was a pile of manure that had been almost rained into non-existence and then run over by a logging truck tire, creating a nearly invisible trail. Having found the source, he went into his marking routine. Our records indicated that that pile had probably been left by his younger brother 10 days previously.

Another role for olfactory perception, investigated in other mammals, is stimulation of aggression. Male mice, normally extremely pugnacious, lose their aggressiveness if olfaction is blocked either surgically or with a chemical masker, such as an atomized mist of perfume (Ropartz, 1968). One price we have found for letting a stallion sniff his own fresh marking manure on the trail is that he shows briefly heightened aggressiveness and will launch a biting attack at another horse ridden too close. To decrease a stallion's agitation at shows from odors of mares ridden in the same class we daub a strong-smelling substance in his nostrils. Doing so also seems to reduce aggressiveness towards other males, who may become even more potent olfactory targets as they sweat up in performance.

There appears to be no literature at all on the ability of horses to learn scent discriminations. In fact, one potential problem with several early visual discrimination experiments was failure to control for the scent of food marking only the correct visual stimulus. Most of the work on scent discrimination and identification has been done with dogs intended for use in tracking or drug location. The capacity of horses in these areas has not been investigated. Having on more than one occasion been brought out of the mountains on a moonless night or in a pea souper fog by a confident horse who appeared to be sniffing its back-trail home, I am curious about their abilities of scent discrimination and identification.

There are many practical reasons for improving human knowledge about the chemo-sensory part of a horse's Umwelt. Safe handling of stallions requires attention to odors

carried on clothing. Aggression and agitation can be decreased by judicious use of smell blockers. Problems with refusal of "strange" water or feed can be averted by paying attention to chemical factors. Foal imprinting, such as recommended by Miller (1991), is at least partly the result of familiarizing the newborn with the smell and taste of future handlers. Horses may be more comfortable if they have their own halters and blankets and be more easily controlled by persons whose hands smell familiar. Some of the variability in level of agitation of an animal may result from odors coming from other animals around it. And since angry, frustrated, and emotionally upset humans release products in their sweat, it may be possible that unintentional olfactory messages can upset or anger the animal as well.

8. Touch: the rider's main route of communication

Tactile perception is another area that has received almost no attention in animal psychophysics. Possibly this is because it is a "contact sense" and, therefore, would seem to yield less information to forming an animal's Umwelt. However, there are several reasons that understanding tactile perception is important for persons concerned with horse behavior. Tactile stimulation is the principal way riders or drivers communicate with their animals. Tactile stimulation is also important in most mammalian species in providing relaxation and forming mutual bonds. Protection against external parasites involves feeling their presence and taking appropriate action. Finally, tactile exploration may be used in the identification of objects and, therefore, valuable to an animal that has relatively poor vision.

In a study of tactile sensitivity, we found it was possible to measure the variation in touch sensitivity thresholds for different locations along the barrel of the horse (Saslow, submitted for publication). Using stimuli developed for gauging human tactile sensitivity, we were surprised to find that horse sensitivity on the parts of the body which would be in contact with the rider's legs is greater than what has been found for the adult human calf or even the more sensitive human fingertip. Horses can react to pressures that are too light for the human to feel. This raises the possibility that human instability in the saddle results in inadvertent delivery of irrelevant tactile signals to the horse and a consequent failure in teaching the horse which signals are meaningful. Horses deemed insensitive to the leg ("dead-sided") may simply have never had the chance to respond to consistent, light, meaningful signals. Similarly, the seeming ability of a well-trained horse to "have ESP" for its rider's intentions, may be instead its response to slight movements or tightenings of muscles that the rider makes without awareness.

"Grooming" is possibly one of the most overlooked potential positive reinforcers when working with mammals. In many species, rhythmic tactile stimulation at the right parts of the body produces a pleasurable and relaxing response. Feh and de Mazieres (1993) identified an area around the withers of the horse in which vigorous grooming would produce a drop in heart rate. Mutual grooming episodes are used as a measure of social bonding in many equine studies (Crowell-Davis et al., 1987; Feh, 1999; Keiper, 1988; Moehlman, 1998). Appropriate tactile stimulation can be used by human handlers for positive reinforcement in training, for desensitization to phobic stimuli, for improving bonding, and may even be useful for improving health.

Biting flies cause both health hazards and emotional distress to horses. Mayes and Duncan (1986) found that feeding patterns in semi-feral horses were strongly influenced by the activity of biting flies. Other investigators have suggested that flies influence choice of habitat (Duncan and Cowtan, 1980), social group size (Duncan and Vigne, 1979), and health (Berger, 1986). Horses have several vigorous responses to detecting a fly landing on their bodies: cutaneous reflex (skin rippling), tail swish, ear flick, foot stomp, head shake, and directed bite. We found a sharp decline in tactile sensitivity in the older horses (>20 years) in our study (Saslow, submitted for publication), similar to that found in elderly humans (Desrosiers et al., 1996). This suggests that the elderly domestic horse may be unable to protect itself sufficiently from flies without the help of blankets, masks and repellents.

The capacity of the horse's lips to use tactile information to discriminate surfaces has not been investigated. Certainly horses can graze in the dark and seem to be able to differentially sort out favored grasses. Before the invention of paste wormer, horse caretakers had to devise elaborate schemes to get worm medicine crystals into their horses. Just mixing the powder into the feed was rarely satisfactory. We had one mare who routinely left a neat little pyramid of crystals on the edge of her feeder after having consumed the grain into which the medicine had been thoroughly dispersed. Tactile discrimination experiments which control for possible olfactory and visual cues would give us information on the degree to which horses can use their lips as ''fingers'' to explore and manipulate their environment.

9. Pain: sensation or response?

One of the most interesting, and confusing, psychophysical areas is the perception of pain. Many different physical simulus modalities can produce ''pain''. Pain sensations have been found to be additive both within and across modalities in a way unlike what is found for other kinds of somatosensory sensation. In humans, for example, low level stimulation of two teeth can produce excruciating pain whereas independent same-strength stimulation of either tooth alone may produce only mild discomfort (Brown et al., 1985), indicating non-linear summation of effects. Some parts of the body seem to be copiously supplied with pain receptors, such as intestines and blood vessels, while others completely lack such receptors, as, for example, the brain itself. Pain perception is thought to be the remnant of an ancient non-discriminating nociceptive sensory system, stimulation of which reflexly motivated the organism to do whatever was necessary to avoid or terminate a possibly tissue-damaging event.

Probably the most interesting aspect of pain perception is its lability. One and the same physical stimulus does not cause the same amount of pain. Context, mood, state of Sympathetic Nervous System activation, and even simultaneous stimulation elsewhere on the body surface can greatly alter the experience of pain in humans. The ''gate-control'' theory of pain suggests that on occasion there is a benefit to the organism of being able to block pain information either by direct neural feedback or by generalized release of opioid neurochemicals called ''endorphins''. Strange psychological phenomena like the placebo effect (reduction of pain because the patient believes a chemically inert pill will help) or the

calming effect of stress-induced eating (rapid eating episodes which occur in anxious humans or animals) have been found to be mediated by endorphin release into the bloodstream.

Lagerweij et al. (1984) found that the curious practice of "twitching" (pinching the horse's upper lip with a tightly twisted loop) to control horse response to mildly upsetting or painful stimulation had a physiological basis. It both decreased the extent of a horse's heart rate reaction to pain and raised concentrations of beta-endorphins in the bloodstream. Also, from our own observation over 30 years of horse handling, twitching as a control method does not produce the resistance to future applications seen with another ancient method, ear twisting (once you have used such an ear restraint on a horse you are unlikely to be able to apply it the next time and may have a "head shy" horse as well).

Acupuncture is another curious pain-relieving maneuver attributed to gate-control by the nervous system of pain. There is evidence in humans that acupuncture effects are at least partly mediated through endorphin release (He, 1987). What is not known is whether the specificity of stimulation points that can produce the effect will be substantiated or whether the amount of effect exceeds what can be achieved through more generalized methods of inducing a client to relax.

Another interesting line of pain research concerns diurnal fluctuations in endorphin release. Hamra et al. (1993) found in the horse that the highest level of beta-endorphin occurs in the early morning and correlates with decreased nociceptive (pain) sensitivity at that time. There may be a best time of day to ask a horse to tolerate painful stimulation.

Although the claim that "animals do not feel pain like we do" has been used as a human excuse for animal abuse (Gavzer, 1989), the antiquity of nociception in the animal kingdom would argue against this. Since the ancient animal response to nociception was to act frantically so as to put a stop to continued stimulation, pain unmanaged is likely to result in fleeing or fighting, either of which can be dangerous when handling a large animal like a horse. The intensity of emotional response to pain perception appears to be based in part on circulating neurochemicals. From what we know as of now, it is crucial for behavioral pain management in an animal to increase endorphin release while decreasing activation of the Sympathetic Nervous System. Being able to reduce anxiety, whether pharmaceutically or by the relaxing actions of a familiar and trusted handler, is important in decreasing pain perception in horses.

10. Hearing captures a horse's attention

Humans attend by moving their eyes no matter what the modality of the alerting stimulus. Horses, however, "attend" by pointing their ears. I have over the years been an expert witness on equine behavior many times in legal suits involving injury and even death. One very striking thing I have noted in hundreds of pages of depositions is the aptness of the term "eye witness". Humans, although they have excellent hearing, seem to concentrate only on what they saw when describing a traumatic event. Often, when matters were pursued, it turned out that unexpected sounds were more likely to have triggered or augmented horse misbehavior.

We are fortunate in the area of horse hearing to have an excellent series of high-quality psychophysical and comparative studies to draw upon (Heffner, 1998; Heffner and Heffner,

1983, 1984, 1986). The horse range of hearing may not go down to quite as low frequencies as does the human, but it certainly exceeds the highest frequencies that can be heard by humans (over 33,000 Hz, or cycles per second, as compared to a human limit of under 20,000 Hz). If we consider the decline in high-frequency hearing that customarily occurs in adult humans (especially males) in our industrialized society, one of the largest discrepancies in horse/human Umwelt is in the area of high-frequency hearing.

There are many situations when, to the horse, the human handler must seem deaf, uncaring, or just plain stupid. Often when trail riding, the first indication we have that other people or animals are in the vicinity is when the horse lifts its head and points its ears. When the horse spooks my human eyes start looking for a visual "cause" only to belatedly realize that the stimulus was the hissing of air brakes or a sudden snap of a branch. Complex sounds with high-frequency components, such as made by machinery, are far more audible to our horses. Parade and show situations where a horse seems unduly agitated can often be made more bearable by using ear plugs (similar to what is done for human athletes trying to maintain concentration while performing with noisy crowds). Since a sound wave can be blocked by obstacles that are thicker than its wavelength, it is relatively easy to block high-frequency sound with small barriers which allow lower frequencies through.

The area of best sensitivity of horse hearing is broad and covers the range of the human voice better than does the dog's. In dog training, men, with lower pitched voices, often prefer to use whistle cues, as is common in sheepherding. However, the indications from horse hearing audiograms are that human vocal commands should be adequate, and whistles or clickers are not an auditory necessity. Provided the horse is trained to the cues and motivated to respond, vocal cues can be at very low intensity especially if coming from a handler close to the animal. The one problem that can arise with use of the human voice for cueing is that human vocal sounds also express emotion, rising in frequency range as well as volume when the speaker is scared or excited. It takes a lot of attention and practice for humans to speak in a "calm voice" when they are not in fact calm.

There is an interesting difference between humans and horses in their ability to pinpoint the source of a brief sound. For low frequencies mammals rely on "interaural time difference" (sound will reach the nearer ear before the one farther away) and both humans and horses localize well with this mechanism. However, it works well only up to about 1000–2000 Hz. For higher frequencies, human hearing makes use of the "interaural intensity difference" produced by the sound shadow of the head. The horse, however, does not seem to have evolved this high-frequency localization capacity; in fact the area of the brainstem which processes this kind of information is small in the horse (Heffner and Heffner, 1986). If the high-frequency sound is prolonged, such as might be the case for a whinny, the horse could potentially localize it with movement of its funnel-shaped ears. However, if it is a brief high-frequency sound, such as the snap of a twig or a warning "sniff" made by another horse, then its exact location could not be pinpointed. Such sharp, brief high-frequency sounds are more likely to be responded to as non-specific alarms triggering the animal's reflex defenses, usually flight in the case of horses.

What is missing from an understanding of the horse Umwelt is the use it makes of sounds in communication, mating, identification, etc. For most species, an animal's hearing capability is matched to the frequencies of that species' most prevalent vocal sounds. The more we know about the acoustic features of a species' calls and the role these play in that

species' behavior, the more we come to know about their hearing. The ethological knowledge that elephant groups appeared to be able to coordinate their social behavior at long distances combined with the physical knowledge that extremely low frequency acoustic stimuli "bend around" natural barriers, like forest and mountains, led to devising special equipment to detect (and generate) subsonic (to human ears) elephant calls. The results of this research have meant that the lower limit frequency estimate of elephant hearing has had to be considerably lowered. Field research on both penguins and bats, who have an incredible ability to locate their young in extremely crowded circumstances, has increased our respect for the ability of animals to recognize particular "voices" out of a cacophony of sound. Work in many species has catalogued the physical qualities and biological meanings of their calls. It is embarrassing that much more information seems to be available about the vocal communication of exotic animal species than for our domestic horses.

Another wide-open area of research on domestic horse hearing is its ability to identify certain auditory stimuli with certain consequences. Although Heffner (1998) suggests that it is difficult for a horse to associate "quality" (non-directional characteristics) of an auditory cue with a spatial response, drivers of horses have been using "gee" and "haw" for centuries, and verbal commands are recommended in combined driving competition. I have also found it useful to teach verbal directional sounds to horses who will be carrying disabled riders or beginners who have trouble coordinating their hands and cannot always produce rein cues at the right time or intensity. And horses can learn to associate certain sounds with certain events. One horse in our barn developed a phobia about a particular veterinarian who had to treat him repeatedly for a very painful leg wound. Years later, although the veterinarian has never again treated this particular horse, the animal still alerts and starts snorting before we humans hear anything coming down the gravel road. His agitated behavior tells us that this is "the vet" and not some other traffic.

Horse handlers need to be aware that horses have a great deal of high-frequency information that humans lack. Some of their inexplicable agitation or "spookiness" may be related to sounds that are out of range of human hearing. Handlers must become adept at "reading" their horse for the presence of these sounds and able to reassure the animal that any source of alarm will be dealt with by the human protector. The handler's voice is a very useful tool for cueing and calming, but humans have to be careful that "tone" of voice does not change unconsciously. Horses can link specific experiences both positive and negative to specific sounds. Sometimes, the key to an animal's agitation may be what it is hearing, if only an "edge" in a stressed rider's voice or the approach of the vet's truck.

11. Vision: do horses and humans see eye to eye?

Vision is one area in which there is very likely to be divergence in Umwelts between horse and human. It is not enough to ask whether a horse can see "as well" as a human. There actually are many aspects of visual perception which are differentially emphasized in different species. For example, the means by which a visual system improves "sensitivity" (ability to detect minimal light levels) are often directly opposed to having good "acuity" (the ability to resolve details of visual pattern). Having the eyes rotated to

the side of the head extends total visual field, an advantage for prey animals, but this reduces or eliminates a frontal overlapping binocular visual field. It is in the binocular visual field where most mammals show their highest acuity and have the possibility of stereo depth perception. Having "color vision" may permit the recognition of some visual targets based on wavelength differences alone but at the same time can mask some contrast distinctions visible to animals with less color vision capability. For some species detection of slight visual movement, such as might signal a predator beginning to move, is crucial to survival while for other species visual identification of a stationary and possibly contrast-camouflaged prey animal has been more important to survival.

Basic to understanding "vision" is recognizing that in vertebrates two visual systems have evolved. The more ancient one is based on rod-like photoreceptors which contain a Vitamin A-dependent chemical. The more recently evolved visual system is based on "cones" which contain a different class of photosensitive chemicals (not Vitamin A dependent) and are differently hooked up to the next stage of visual processing. Scotopic (dim-light) vision resulting from activity of the rods is very sensitive to both light level and movement, but is not optimally connected to the central nervous system for seeing details of the visual image. It responds well to small contrast fluctuations but does not produce color perceptions. Cone-based photopic (bright-light) vision, which requires much higher levels of illumination to function at its best, has developed for detail vision and detection of much higher contrast differences.

Different species of mammals have different mixes of scotopic and photopic visual capabilities. Primate retinas have relatively high concentrations of cones overall and a specialized high-acuity area of the retina, the fovea, which has only cones. However, horses have a lower proportion of cones to rods and no area of cone-only concentration. The electroretinogram of the horse eye is dominated by rod input. These anatomical and physiological aspects of the horse eye imply an animal whose overall ability to see is likely to be shifted towards the characteristics of scotopic vision and whose best visual functioning is likely to be at lower levels of illumination.

The rods and cones of the retina project to ganglion cells which summate the information and relay it to the brain. The lower the ratio of ganglion cells to photoreceptors, the more sensitive an eye is to minimal light levels but the less able the visual system as a whole will be to respond to high spatial frequencies (visual detail). Compared to primates, the horse retina has a very thin ganglion cell layer (Prince et al., 1960) indicating, again, that overall horse vision will be less able to give information about visual detail, especially in a stationary scene, than will the human.

In fact our human perception of the specific types of information vision can provide is dominated by less than 5% of our retina. Primates are atypical among mammals in having a "fovea" or area of concentration of closely packed, skinny cones which are in a 1:1 ratio to ganglion cells. Because rods are eliminated from the fovea, this area operates only at relatively high levels of illumination. The primate fovea produces high-acuity trichromatic color vision and, because it lies in the center of the binocular field, precision stereo depth perception as well. The impression that the information gathered by this small part of the retina constitutes most of what is "vision" is maintained for primates by having an exceedingly mobile eye which rolls quickly back and forth in the socket to aim this small fovea at whatever small portion of the visual scene is of interest.

However, when the human eye is fixated in a research or clinical setting, it is easily determined that our customary "vision" deteriorates rapidly with distance from the fovea, losing detail, stereo depth perception for very distant objects, and "normal" color but remaining sensitive to movement and contrast. The horse does not have a fovea and also the horse's eye does not roll easily in its socket. The overall proportion of cones is low and its photoreceptor to ganglion cell ratio high. Human peripheral vision is probably a better approximation of most of what a horse can see.

Other characteristics of the horse eye also indicate likely differences in visual perception. The upper half of the retina is backed by a "tapetum", or shiny layer lacking in the human eye. This layer will increase sensitivity for light reflected from the ground. Most light that hits a retina passes on through the photoreceptor layer without effect. If a tapetum is present, however, stray photons get a second chance at being captured as they bounce back. A tapetum increases the sensitivity of an eye to light overall but the resulting light scatter decreases ability to pinpoint the original source of the light, again an aspect of the horse eye that increases sensitivity at the expense of acuity. The unusually large size of the horse eye, a characteristic seen in nocturnally active animals who make use of vision, also suggests that it is an eye specialized for dim-light vision. The horizontal shape of the horse's pupil and the ability, with the assistance of the corpora nigra, to close it down to a mere slit is both a protection against glare and an indication of a species evolved in a landscape without cover. However, the effects of this unusual pupil construction on stimulus visibility are not known.

Horse retinas do have a horizontal "visual streak" in which the ganglion cell concentration increases somewhat (and it is assumed that the photoreceptor to ganglion cell ratio decreases) but it is a mistake to liken the vision in this area to that seen by the human fovea. The retinal histology (Hebel, 1976) as well as the little data we have on horse visual acuity (Timney and Keil, 1992; Saslow, 1999) would indicate that at their best, horses respond preferentially to lower spatial frequencies in a visual scene than do humans (i.e. see outlines rather than details). Harman et al. (1999) in attempting to show the difference between the extensive horizontal area of "best vision" for the horse and the small circular area of "best vision" for the human, produce pictures that are somewhat misleading by having both views show the same amount of visual detail. Horse retinas, even in the visual streak, simply do not provide the rest of their visual system with the quality of daytime vision available to primate foveas. Unfortunately, this mistaken impression that horses have vision as clear as humans for a strip in front and along the two sides of their body has already made its way into the popular press (Kilby, 2000).

Horses do, depending on their breed, have a small area of binocular overlap. Recent research (Timney and Keil, 1999) indicates that within this area, they may be able to use stereo depth cues in addition to the monocular stationary and movement depth cues available to each eye by itself. But the distances over which these retinal disparity stereo cues will work are dependent ultimately on the animal's acuity in the overlapping fields. And from what we currently know, the horse's photopic acuity is much less than its human handler's.

For better understanding of horse vision, we need to have more histological and electrophysiological data. As mentioned before, researchers still must base their interpretations on Hebel's 1976 counts of ganglion cell densities. We still infer photoreceptor to

ganglion cell ratios by comparing thickness of retinal layers. Accurate information about the absolute and relative densities of rods and cones across the horse retina is not yet available. Neither is the important information about variation in size of ganglion cell summation fields at different retinal locations. Since a great deal is already known about the relation of nervous system structure and function to visually guided behavior in vertebrates, such anatomical and physiological information would give valuable clues as to the most meaningful behavioral studies to undertake.

Psychophysical information is still needed on the basics of horse vision. What are the differences in their visually guided behavior between photopic and scotopic illumination conditions? What is the variation in acuity and movement sensitivity at different locations in their visual fields? What is their capacity for visual recognition of stimuli at different points of the visual field? How does their vision differ between the small area of binocular overlap and the much larger monocular areas that occupy most of their visual fields? How does vision in fact differ between the area subtended by the visual streak and the areas above and below? What are their scotopic and photopic luminosity functions (information basic to interpretation of color discrimination data)? How does their head position affect what they see? Do their bobbing head movements increase their ability to recognize stationary visual targets?

Even though vision is the most researched of the equine senses, there are still large gaps in our knowledge. Human handlers need to be constantly aware that the horse's visual information is different from their own, especially under bright-light conditions. The horse has a much wider visual field, but the quality of its vision, compared to a human's, is not good over most of this area. The vision it has down its sides would seem to function better for warning than stimulus identification. What seems to be the inexplicable "spookiness" of the horse may often be a reasonable response to what it sees.

12. How do you cope with different Umwelts?

The keys to safe and productive handling of an animal with such a different Umwelt are two-way communication and trust. We cannot make horses feel, hear, smell or see things the way we do. However, we can teach them that if they follow our lead, however, incomprehensible it may be at times, nothing bad will happen. For daytime vision, we must convince our horses to let us be their trusted guide dogs. On the other hand, for high-frequency sounds, we must learn to let the horse be our hearing aid. For the rich olfactory world to which we are largely insensitive, we have to bow to their superior noses and avoid odors which offend or agitate them. And, especially, we must respect their integration of exquisite tactile sensitivity with a muscle power that can override any of our commands if we neglect to make our requests meaningful, consistent and polite.

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