The Horse's foot as a Neurosensory Organ: How the Horse Perceives its Environment

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Chapter 5

The Horse's foot as a Neurosensory Organ:

How the Horse Perceives its Environment

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Introduction

The horse's foot is the primary avenue for the horse to obtain information about the physical features of the ground surface upon which it stands and moves. The horse gains access to this information via the nerves and receptors, which are specialized for sensing specific information that is detected by the foot. This information is then transformed into electrical activity which is conveyed along nerves in the horse's legs to the central nervous system (CNS), including the spinal cord and brain. Within the spinal cord, the generated nerve activity becomes incorporated into the different reflexes needed for movement, postural adjustments, and/or for protective mechanisms. **Some of** this activity is also sent to the brain for perception. Free nerve endings convey painful sensations while other sensations such as touch, vibration, etc are initially detected by what are called mechanoreceptors before the information is transmitted to the spinal cord. The wealth of sensory structures need to be activated by the physical deformation of the nerve endings and do not necessarily require conscious perception to respond immediately to stimuli (Figure 2). These sensory structures detecting touch and vibratory stimuli are important to enable smooth transitions between movements of the joints and limbs during a performance, as well as maintain the appropriate postural stance.

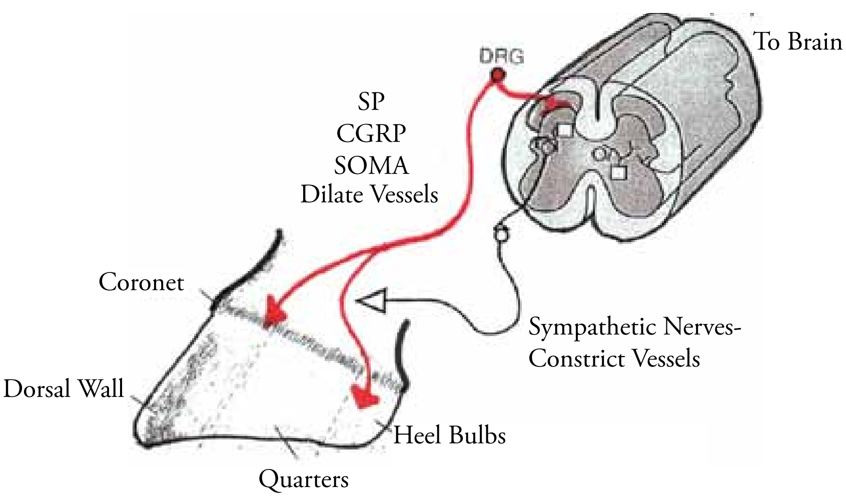


Figure 1: Schematic drawing of a cross section of a spinal cord and the sensory nerves passing from the horse's foot to the spinal cord to enter into the various reflexes. A sensory nerve (RED fiber) consists of neural cells located in the dorsal root ganglion (DRG) and has two long fibers with one passing to the foot and the other passing into the spinal cord. The many different sensations that are detected and perceived by the horse's foot are conveyed to the spinal along these nerve fibers. When this sensory information reaches the neural processing centers of the spinal cord, then some of the information is incorporated and used in the spinal cord reflexes that are so important for locomotion. These spinal reflexes aid in the contraction and extension of the limb muscles as well as the sequence of muscle contractions. Other components of this sensory information may pass to the brain for perception of what the specific stimuli and sensations are being detected by the foot. A third function of these sensory nerves is that when activated they also may have a local effect within the tissues of the foot, as these sensory nerves will often release some of their neurotransmitter chemicals into tissues locally. Within the many nerve cells of the DRG are cells each having different chemicals or transmitters, that enable the nervous system to be able to communicate with other nerve cells. These chemicals are many, but only a few are listed here, as we have dealt with these sensory neurotransmitters directly: SP: substance P; CGRP: calcitonin gene related-peptide; SOMA: somatostatin; and more than 12-18 other peptides and small proteins that act as neurotransmitters in being able to excite or inhibit other nerve cells. The other nerve fiber system present in the foot of the horse is those nerves that are part of the sympathetic nervous system (two nerves in black). The sympathetic nerves are involved in the "fight or flight" response when we the horse is startled and are important in providing information to the smooth muscle fibers surrounding the blood vessels within the foot. Nerves fibers pass to skeletal muscles, but there are few-to-no muscles present in the horse's foot. Robert Bowker files.

Schematic drawing showing sensory nerves innervating the horse's foot. The fibers from the spinal cord pass via the palmar digital and palmar metacarpal nerves to the horse's foot. Each of these nerves (the medial and lateral branches and the sensory nerves to the dorsal and more proximal foot appear to convey most all sensations that we can identify within the horse's foot. They permit a wide variety of sensory information to be conveyed to the spinal cord from the foot, and each one has different or several effects upon the microvasculature and other tissues within the foot. Robert Bowker files.

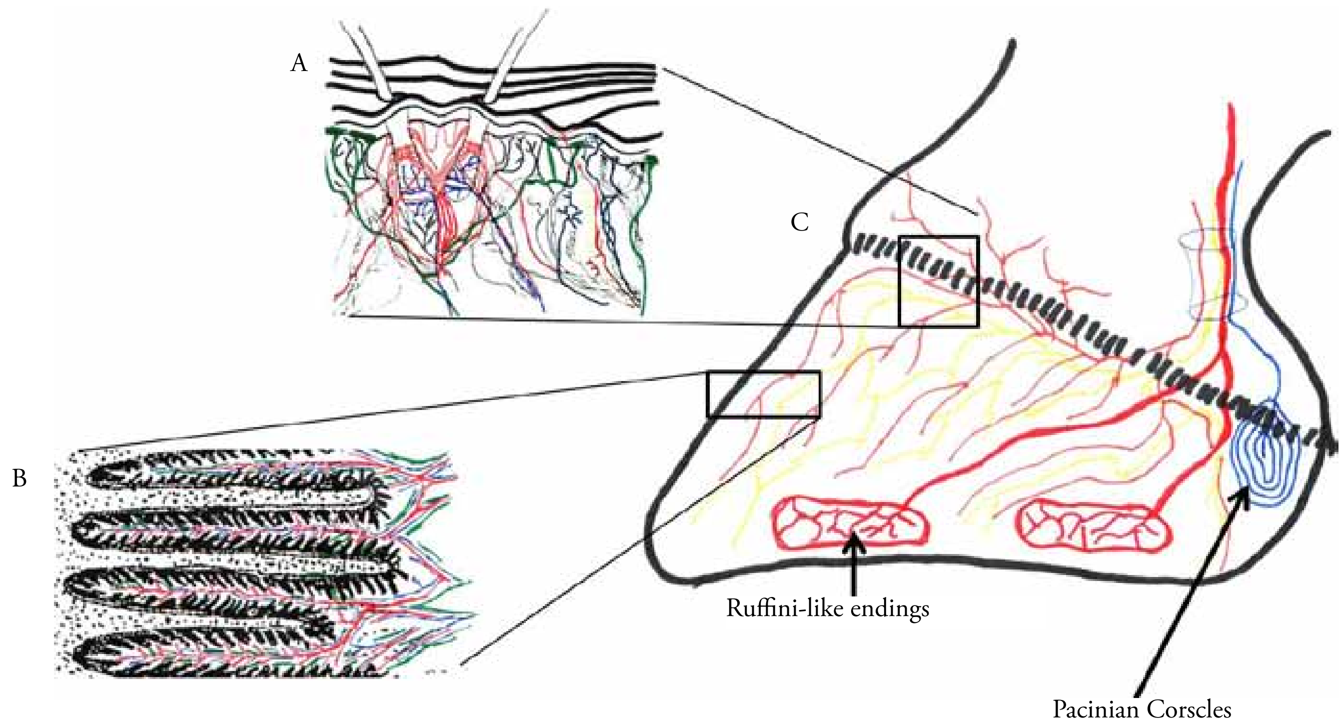


Figure 2A: Superficially, within the skin and areas of the coronet, many of these sensory nerves are present. Within the skin and surrounding the hair follicles are: tactile (touch) nerves (RED) that are very responsive to any movement of the hair shaft either by the wind, insects etc. There are other tactile nerve fibers (YELLOW) within both the epidermal and dermal layers and Merkel cells (GREEN) within the basal epidermal layers. This information can be carried to the spinal cord and to the brain for perception. Physiologically, Merkel cells detect tactile or very light pressure sensations (NOTE: differentiation of these two sensations is difficult both physiologically and behaviorally). From the animal's perspective these sensory data are transmitted and incorporated into different reflexes of the spinal cord during various gaits (walk, trot, canter, etc) and during more complex movements (jumping over fences and negotiating objects on the ground surfaces). Interestingly, placement of light-weighted anklets upon the fetlock can enhance the movements of the distal limb of the horse by activating these tactile receptors. Pain fibers (BLUE) can also be activated but usually only during damage or injury to the tissues. These thinly myelinated fibers are present around the hair shaft as well as are distributed throughout the dermal and epidermal layers.

Figure 2B: Within the hoof wall, both tactile and light pressure fibers are present in the form of free nerve endings and Merkel cells. Pain and thermal fibers are also evident, when staining with specific identifying markers, such as Substance P and Calcitonin gene-related peptide. Pacinian corpuscles are not evident in the corium of the hoof wall.

Figure 2C: Similar structural elements are present within other areas of the foot, potentially for detecting the sensations of touch, pressure, pain and thermal energies. Light pressure/vibration sensations can be detected by Pacinian corpuscles (BLUE) at the heel bulbs and more deeply within the foot, while light pressure/tactile fibers and receptors (Ruffini endings) are present around the major nerves passing to the horse's foot and within the dermal areas of the sole and heel regions. These latter two receptors may be activated during movements with the foot contacting the ground surface or during times when these high energy vibrations are being transmitted through the ground to be detected when the horse's foot is stationary. PDN: These released chemicals from the sensory nerves can dilate the vessels, promote edema formation, attract white blood cells, etc, during inflammation.

The sensory structures in the horse's foot are activated by the physical deformation of the nerve endings and do not necessarily require conscious perception to respond immediately to stimuli.

Other nerves conveying pain are the ones that often need to be desensitized by local anesthetic to localize the origin of pain during a lameness examination. However, the horse has little regard for the pain nerve fibers (i.e. normal horses do not think about pain unless they are in pain, when it becomes a focal point of attention). The horse uses mainly the mechanical stimuli to get around the environment, as this mechanical information permits the horse to smoothly negotiate the varied surfaces the foot encounters as it gallops over the countryside. Knowledge of the types of sensory nerves and receptors present within the distal limb and foot are all-important ingredients to determining and appreciating the rich neurosensory apparatus of the horse's foot. **By knowing the locations, distribution, and the resulting behavioral and/or physiological effects of these many types of receptors in the foot when stimulated, one can begin to understand how the foot affects the upper limb and body, including the axial skeleton and neck, as well as vice versa!** As you will see, the horse's foot has the same variety of nerve types that we do in our own hands and feet. *Most of these nerves do not conduct pain, but they do provide the critically important sensory information needed by the horse's CNS for the many reflexes involved in the movements, as well as for the sensory awareness that the horse needs as a prey animal regarding its surroundings. These mechanoreceptors also produce local effects within the tissues, such as improving blood perfusion through the foot; these local effects within the tissues are perceived as "being comfortable" when these effects occur in humans.* For this reason it becomes an interesting notion that the horse does in fact seek out areas in its environment that are "comfortable" from a horse's perspective.

In other creatures, any local response in the foot to mechanoreceptors may affect the different vascular beds. This suggests that there is *a coordinated and complex activity by the nervous system to actively alter regional blood flow and perfusion of different tissues, depending upon the stimulus.* Such physiological changes in tissue perfusion are beneficial, as they enable the foot to dissipate the energy during ground impact and to provider support during the stride—to interact with the environment, to protect the foot and to alter the sensory-perceptive capabilities by changing the sensitivity of the receptor—either to enhance or reduce its sensitivity. By enhancing our understanding of what these nerves and receptors are, where they are located within the foot, and how they may produce their physiological effects both in the CNS and locally, we can then value their beneficial effects for the horse, as well as for us as hoof care professionals in the prevention and treatment of lameness problems. Thus the purpose of this chapter on the neural structures within the horse's foot is to provide information as to the types and locations of these various sensory structures, to show how you may employ them to improve foot health, and to also show how these same elements appear to be utilized by the horse for detecting and examining stimuli in its environment.

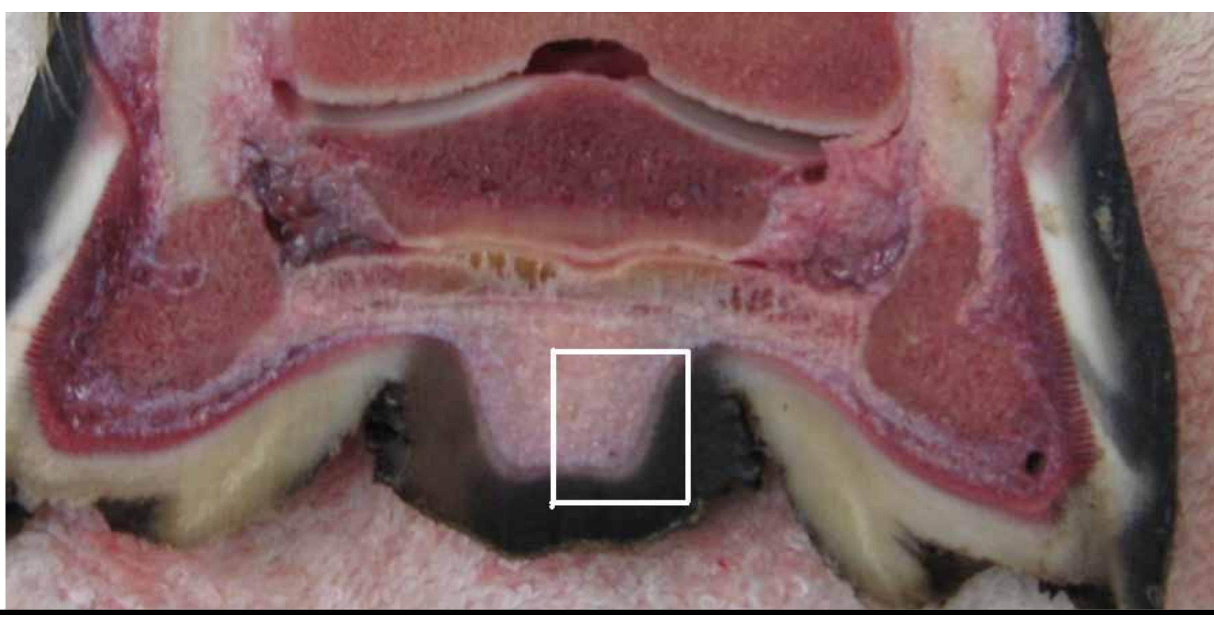


Figure 3A: Cut section through frog showing the epidermal covering as well as the internal dermal and subcuteal tissues. Higher magnification of this area is shown on the opposite page in figures 3B and 3A. Robert Bowker files.

Location of the Nerves

The feet of most mammalian species have contact with the ground via their hooves and/or foot pads, which are covered by very densely cornified epidermal layers with underlying dermal and deeper subcuteal layers (Figure 3). The hardened keratinized horn protects the inner workings of the foot or fingers while the internal tissues function to support, nourish, perceive stimuli and dissipate any potentially harmful impact energies. These tissues must be capable of protecting the distal limb of the animal, and must also provide a means for the animal to obtain information about its surrounding environment. Internally, the subcuteal regions within the foot often are a mixture of collagen, fibrous, fat and elastic fibers forming a complex and interwoven tissue network. Within this network is a more "primitive tissue" called myxoid tissue, which has as one of its characteristic traits, the ability to adapt and change in response to environmental stimuli.[25] One such adaptation is the formation of fibrocartilage.[8] It is within these tissue layers that the various sensory nerves and receptors are embedded for detecting the different types of mechanical, painful and thermal stimuli that the foot may come in contact with.

Pain Receptors

Most of the known sensory receptors have been subdivided into several broad categories based upon their physiological responses when presented with a stimulus. These sensory receptors include pain, heat and cold and mechanical receptors. The **pain receptors become active when tissue damage occurs**. In humans, painful sensations are subjective and are usually defined as being an unpleasant sensory and/or emotional experience. In animals, we rely on behavioral responses of withdrawal or escape from the offending stimulus to indicate painful sensation. Pain thresholds will vary from individual-to-individual, and from animal-to-animal requiring a behavioral response. So a stimulus that causes a painful reaction in one animal may not cause a reaction in another animal. In the horse, activation of these painful sensations is observed and utilized during a lameness examination when the horse is experiencing sufficient discomfort to alter its movement sequence or to acknowledge discomfort during the application of hoof testers. These behavioral responses are usually referred to as **physiological pain**. Activation of these pain receptors supersedes the influences of the other mechanoreceptors in determining the locomotion pattern. The pain

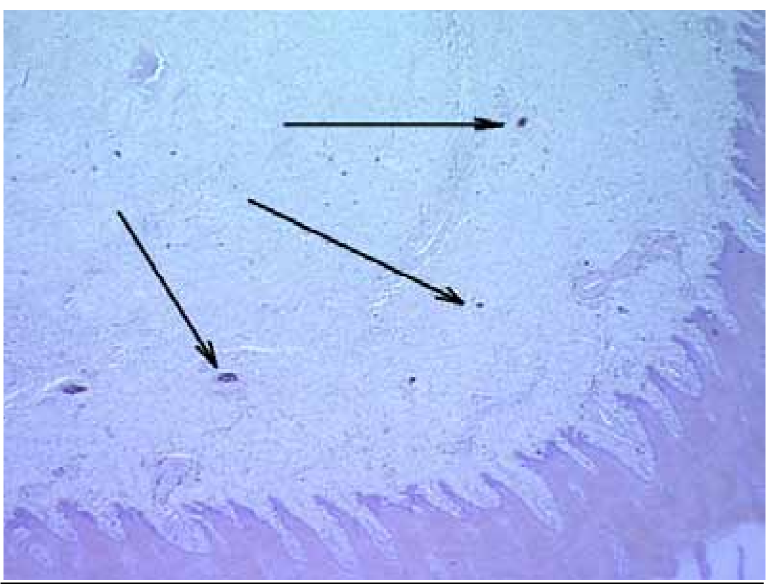


Figure 3B: Histological section of frog that has been stained to identify the many sensory nerves passing through the caudal to rostral frog tissues. The arrows indicate several of the large sensory nerves that convey tactile sensations, as well as the many small myelinated fibers containing SP and CGRP that regulate tissue perfusion. These labeled nerve fibers are well distributed throughout the frog corium, and small branches continue along the smaller vessels as they enter the epidermal tubules (enclosed area). Robert Bowker files.

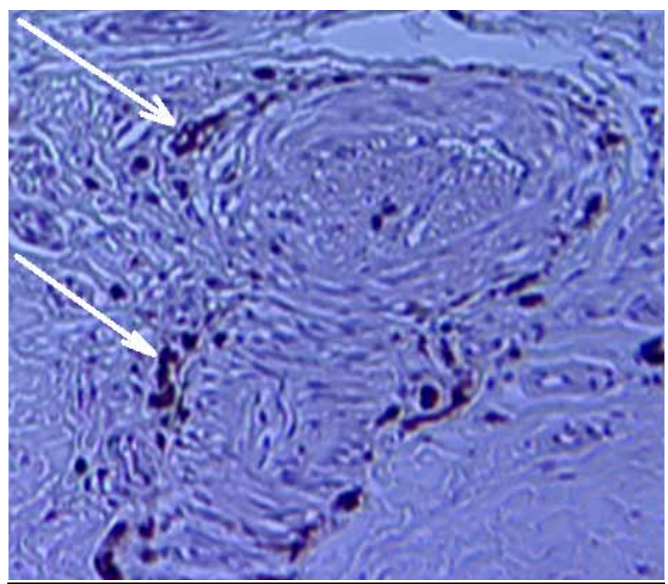


Figure 3C: Higher magnification of the thick-walled microvessel can be seen to have dense nerve fibers around the vessel (small white arrows) as it passes into the epidermal tubule of the frog.
Robert Bowker files.

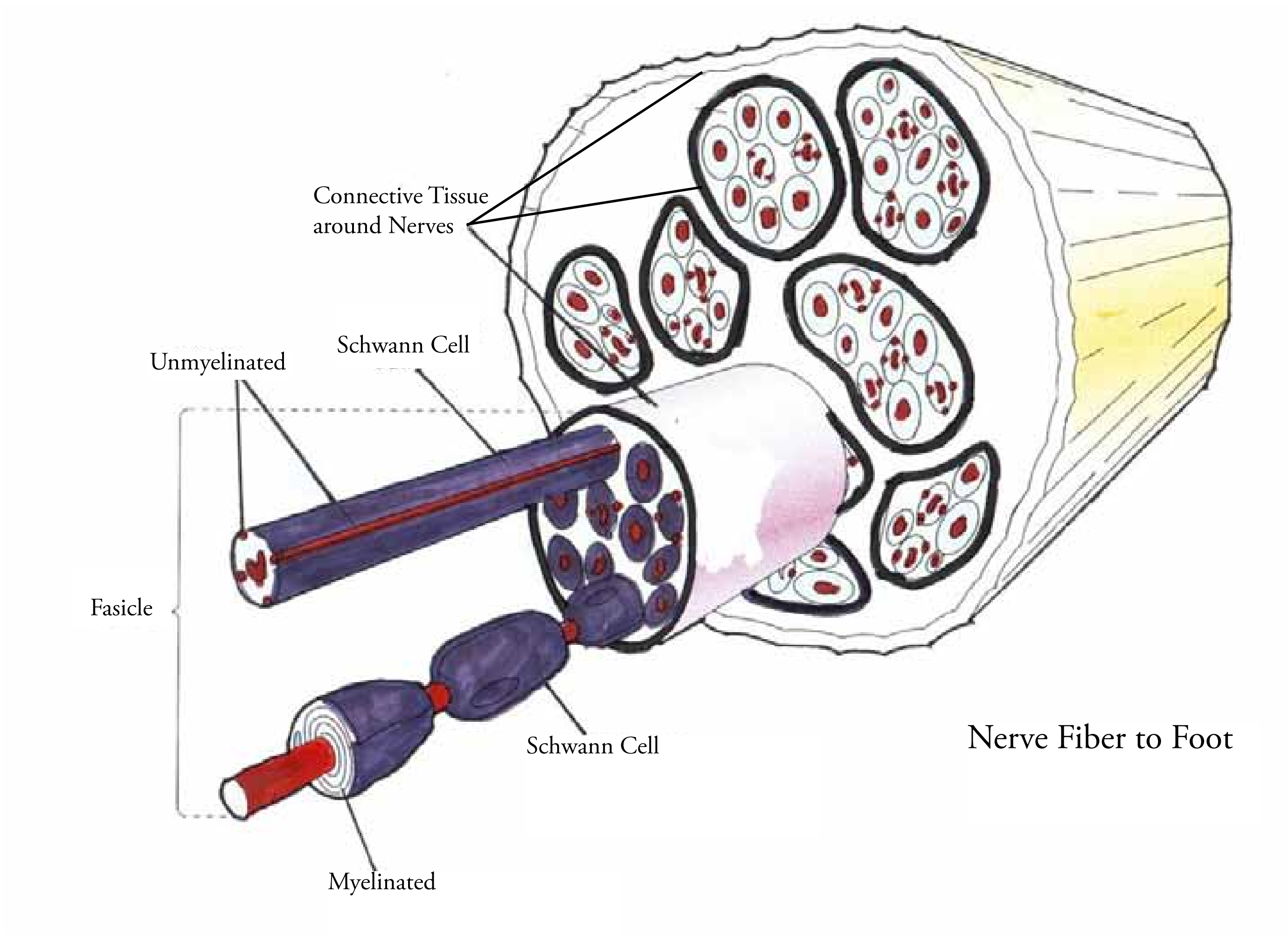


Figure 4: Schematic drawing showing a spinal nerve passing to the equine foot and its composition of both myelinated (fast conducting nerves) and unmyelinated nerves (slower conducting nerves). The thicker myelinated nerves have a fatty substance around the fibers which insulates the individual nerve or axons (RED), allowing the electrical activity to be conveyed rapidly to and from the spinal cord. The myelin is colored purple to blue in the drawing and is produced by cells called Schwann cells. The smaller nerve fibers represent the unmyelinated nerve fibers, which are similar to axons, being embedded in the myelin rather than being snuggly wrapped like a jelly roll by a thick covering of myelin. In the horse, the nerves to the foot have approximately 4-5 unmyelinated nerves for every myelinated nerve fiber. The myelinated nerves convey tactile and vibratory information to the spinal cord while the unmyelinated nerves contain the peptides which are so important in mediating local effects within the tissues of the foot. Adapted from Ransom, BR, Organization of the nervous system, In: W. Boron and E. Boulpaep, Medical Physiology, a cellular approach, Saunders, Philadelphia, 2003, p. 277.

receptors usually are the fine, free nerve endings with a thin wrapping of insulation (i.e. a fatty substance called myelination) (Figure 4). These "pain" fibers penetrate into the different tissues, through the basal layers of the epidermis and extend toward the surface (Figure 5). Some of these fibers appear to extend into the very basal layers of the stratum lamellatum. The role of myelination as an insulator becomes important when these pain fibers are activated. We have all experienced the pain reflex changes, such as when you reach for a hot pan on the stove: you get the instantaneous reflex withdrawal of your hand from the hot pan and then about a second later you feel the burning sensation of your hand. The quick withdrawal of your hand is carried out by rapidly conducting nerve fibers (i.e. they have thick insulation around these nerves) passing to the spinal cord and back to the hand's withdrawal muscles. In a delayed response of a second or two, one begins to perceive a burning sensation within the tissues of the hand. This sensation is carried by the pain fibers (thin layer of insulation which conveys the neural activity to spinal cord very slowly). Fortunately, Mother Nature had us wired this way for our own protection. If it were the reverse (i.e. the slow pain fibers were important for hand withdrawal by conscious thought), we would all have probably cooked our hands when we were very young whenever we put them on anything hot, as we would not have been able to move them quickly enough prior to significant tissue damage.

Thermal Receptors

In a similar structural mode, a **thermal receptor** also represents "naked" or thinly myelinated nerve endings, but these nerves respond to temperature changes (both absolute and relative), rather than to tissue destruction. These temperature-sensitive nerves respond mainly to either warm or cold temperatures within the innocuous ranges, rather than at the extreme temperatures that cause tissue damage. When tissue damage is done, pain fibers are activated. Within the horse's foot, little is known regarding the presence of thermal receptors and their potential biological responses. However, anecdotal evidence does suggest that thermal receptors may be present within the tissues of the horse's foot, as many riders have mentioned that during the hot summertime when they are riding on a beach the horses respond by trying to avoid stepping on the very hot sand. While the response capabilities of the horse may be altered by external or environmental influences, the thermal-sensitive nerves are more or less capable of responding to temperature changes despite being within the enclosed keratinized hoof.

Mechanoreceptors

The third type of sensory receptors within the horse's foot is the **mechanoreceptor**. These types of receptors are present within the dermis (corium), where blood vessels and connective tissue are located. **They become activated when a physical deformation of the skin and the underlying tissue occur, rather than tissue destruction or temperature changes**. This deformation results in a series of electrical events being generated and conveyed to the spinal cord and brain. Generally, there are several different types of mechanoreceptors, which are activated by different physical stimuli, but are usually not activated by painful stimuli, or ones that cause tissue damage. These receptors respond to a range of stimuli from light physical touch (i.e. mosquito landing on skin hairs or a light breeze), to vibrational energies (i.e. foot impact when the heels hit the ground and earth vibrations during earthquakes) and/or to deep pressures (i.e. foot loading while standing or being supported on small area of foot), to name a few.

Each of these three sensory mechanoreceptors is selectively sensitive to different physical stimuli, or energies; in other words, they only respond to one or two types of stimuli, or energies. In this manner, activation of different but specific receptors or activation of a combination of several types of sensory receptors will produce differing sensations, as well as a wide range of individual sensations that can be perceived by the horse. For example, if a rapid pressure was applied to the palms of your hands (i.e. hand clap), the touch, pressure and even vibratory receptors may all be activated in that brief moment. However, the perceived sensation may be a combination of activating all of those receptors, as opposed to the perception of three different sensations of touch, pressure and vibration. These more complicated stimuli begin to be organized and perceived in the higher brainstem areas and even cerebral cortex.

These combinations of energized receptors are still being investigated. The sensory field activated by a stimulus can have a small or large area of detection, especially in the deeper tissues of the foot. In humans this idea is similar to a small localized area on our fingers for more precise localization, versus a larger area that would be perceived if activated by the same stimulus if it were on our backs (i.e. less precise localization). These same effects in sensory biology are probably occurring in the horse. Here, the same stimulus applied to the foot (i.e. small stone with small percentage of weight or with all weight being applied) may activate the same receptors, and have a small receptive field. The smaller field would be important for locating the specific stimulus while a broader field could be activated if the stimulus strength was greater due to its effects upon deeper tissues (i.e. pressure), resulting in a less precisely localized stimulus.

The different mechanoreceptors are not equally distributed throughout all areas of the horse's foot; they are regionally localized to restricted areas of the foot. This observation indicates that some receptors may have specific roles in detecting and informing the horse about its environment during movement and stance postures, while others distributed throughout the foot would be important for most interactions with the environment and less critical for specific activities. We will briefly discuss where and what these sensory nerves and receptors are, and how the horse appears to utilize these receptors.

The horse's foot is really a neurosensory organ, as its very rich supply of types, and diversity of chemically identified nerves seem to be holding all of the tissues together.

Microscopic Distribution Of Nerves Within The Foot

The dissection of these sensory nerves in the distal limb and foot of the horse provides only a limited view of the foot's extensive sensory innervations. As we dissect below the pastern region, the sensory nerves become smaller and smaller, making them difficult to see with the naked eye. However, they seem to really multiply under the microscope as the sensory nerves become small, thin fibers, with many forming large or extensive "flower spray" endings that spread out the effective area of nerve innervations. When we examine the foot tissues under a microscope, the sensory nerves are found to be almost "everywhere", suggesting that *the horse's foot is really a neurosensory organ, as its very rich supply of types, and diversity of chemically identified nerves seem to be holding all of the tissues together.* These observations imply that the horse's foot is very sensitive to many and different types of sensory stimuli in its environment, being similar to the dense innervation of our own fingers. The many different types of stimuli in the environment, once detected, will send this information to the spinal cord to become incorporated in the spinal reflexes needed for stance or movements, and perhaps affect the overall behavior of the horse, or the sensory information may affect the tissues locally and be influencing the foot's physiology of blood flow through the veins, small arteries, lymphatic vessels, and also the internal milieu or "environment" of the foot.

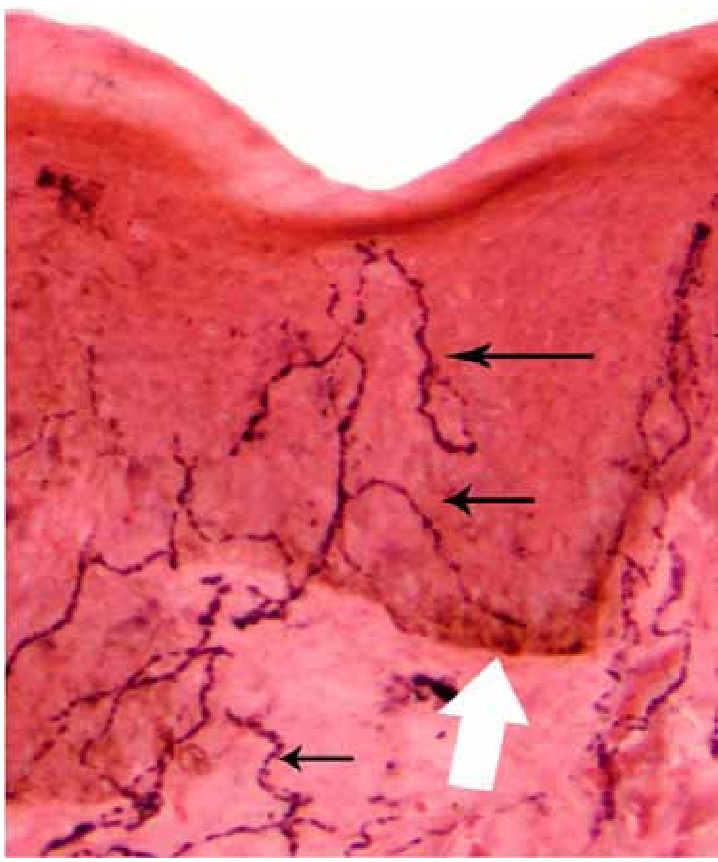


Figure 5: Histological section of equine epidermis showing sensory nerves containing Substance P (SP) as a neurochemical transmitter within the nerves. The black beaded fibers can be seen to pass from the underlying dermis (light color) and pass into the upper levels of the epidermis. The white arrow marks the border between the dermis and epidermis. The smaller black arrows mark the sensory nerve fiber at different locations within the skin. Robert Bowker files.

Once stimuli are detected, the sensory nerves convey activity to the spinal cord at rates depending upon their degree of insulation (myelination). Relatively thick myelin sheaths convey sensory information faster than the thinly insulated nerves (remember the example of the hot pan?). This information and its rapid transmission from the foot to the spinal cord is necessary for its incorporation into the spinal cord reflexes and the centrally programmed generator (CPG) in the spinal cord and brainstem for locomotor activity (walking to galloping) (Figure 6). The CPG is a group of rhythmically-firing nerves cells in the spinal cord that coordinate the specific flexor muscles and extensor muscles of the front and hind limbs to contract and extend together with the muscles of the back and neck. The CPG receives sensory information from the feet and all of the ligaments, tendons and the like from the limbs and back and incorporates this information and then processes it to be sent back to the flexor and extensor muscles of the limbs and back musculature rapidly. This integration of sensory and motor information permits the horse to race along uneven ground surfaces and over fences with little thought effort. The sensory side of this equation seems to be more important as there are approximately four times more nerve fibers with thin or relatively little insulation as compared to the thicker myelinated motor nerves.

So why did Mother Nature provide the horse's foot with so many sensory nerves with different types of fibers and neurotransmitters? Unfortunately, the answer to this question remains elusive; however, each of these neurochemicals has the capability to affect various tissues slightly differently to carry out their effects and purposes. For example, if one or more of these sensory neurotransmitters are affected by disease, then there is another neurological system present that *pick up the slack* so to speak and carry on with similar sensations and interactions with other tissues.

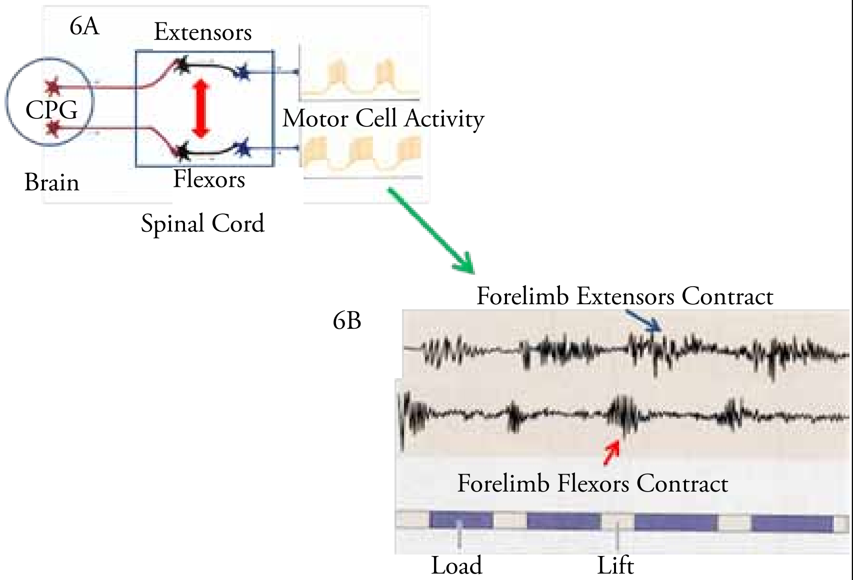


Figure 6A schematically illustrates the Central Program Generator (CPG) present in the brain (two brown cells) and in the spinal cord (blue blocked area) of the horse. This "locomotory generating and coordinating system" is responsible for providing neural activity to the spinal cord from the brain (1) for coordinating the movements and the muscular contractions of the forelimb and hind limb with each other and among the four legs, and (2) for incorporating the sensory information from the environment necessary for the limbs and back musculature to adjust their activity with each step. In the brain, whenever the horse walks, runs, etc, the CPG cells become active and send their neural activities to all levels of the spinal cord. This nerve cell activity coordinates the contractions of the cervical and lumbar muscles of the back and neck with the muscle contractions of the limbs, as well as between the forelimbs and the hind limbs.

On one side of the spinal cord, this alternating neural activity passes between the flexor motor cells (flexors) and the extensor motor cells (extensors) controlling and coordinating the respective muscle groups of that limb. These nerve cell activities are responsible for not only coordinating the proper sequences of the muscular contractions within the same limb (Motor cell activity), but also telling the muscles how much to contract.

In figure 6B, this nerve cell activity in the spinal cord can be seen in graphical form of the muscular contractions within the same limb, as alternating contractions and relaxations of the respective extensor (blue arrow) and flexor (red arrow) muscles are recorded. When the extensor muscles contract, the forelimb is on the ground and supporting the weight of the animal (Load-blue color). When the flexor muscles contract the forelimb is lifted off the ground and there is no weight being supported (Lift-white color). This reciprocal contraction and coordination of the different muscles within the same limb is due to the CPG within the spinal cord and brain. In addition, this alternating neural activity is occurring between the two forelimbs, as well as with the two hind limbs, and results in a well integrated, but complex "locomotory generation pattern" of limb movements.

This basic nerve activity in the brain and spinal cord will change in its overall level of neuronal activity, depending upon the speed and gait of the locomotion pattern of the horse. This level of activity can range from low cell firing at a walk to high bursts of activity during a full gallop. The sensory nerves of the forelimb are composed of both the thinly myelinated nerves (painful sensations) and the thickly myelinated fibers (touch, pressure, proprioception and vibration) and can provide information about the ground surface during these movements. These sensory inputs are detected and perceived when the horse is walking or running and then are conveyed to the spinal cord. These sensory inputs can then influence and change the spinal activity of the CPG. This sensory input is critical to the proper functioning of the spinal cord generator complex for coordinating movements as it will inform the nervous system as to how much and how fast the muscles of both the limbs and back will need to contract to support the horse when moving over the ground surface. Robert Bowker files.

Clinical and Physiological Significance

The wealth of sensory nerves innervating the distal limb and foot strongly suggests that the horse's foot is a very sensitive organ for detecting the countless and diverse environmental stimuli, as these stimuli are incorporated into local reflexes and also are processed at higher levels of consciousness for the horse's perception. The broad range of sensory receptors and nerve fibers further illustrates that the foot is one of the primary means by which the horse gains information about its environment, not only upon the surface that the horse walks on but also from deeper regions within the ground surface. Without these sensory inputs, the CPG of the brainstem and spinal cord could not function appropriately. Each of the many types of nerve fibers and their specific chemicals contribute a small piece to the entire puzzle of the neurobiological control of equine movement and sensory perception permitting the horse to negotiate within its environment.

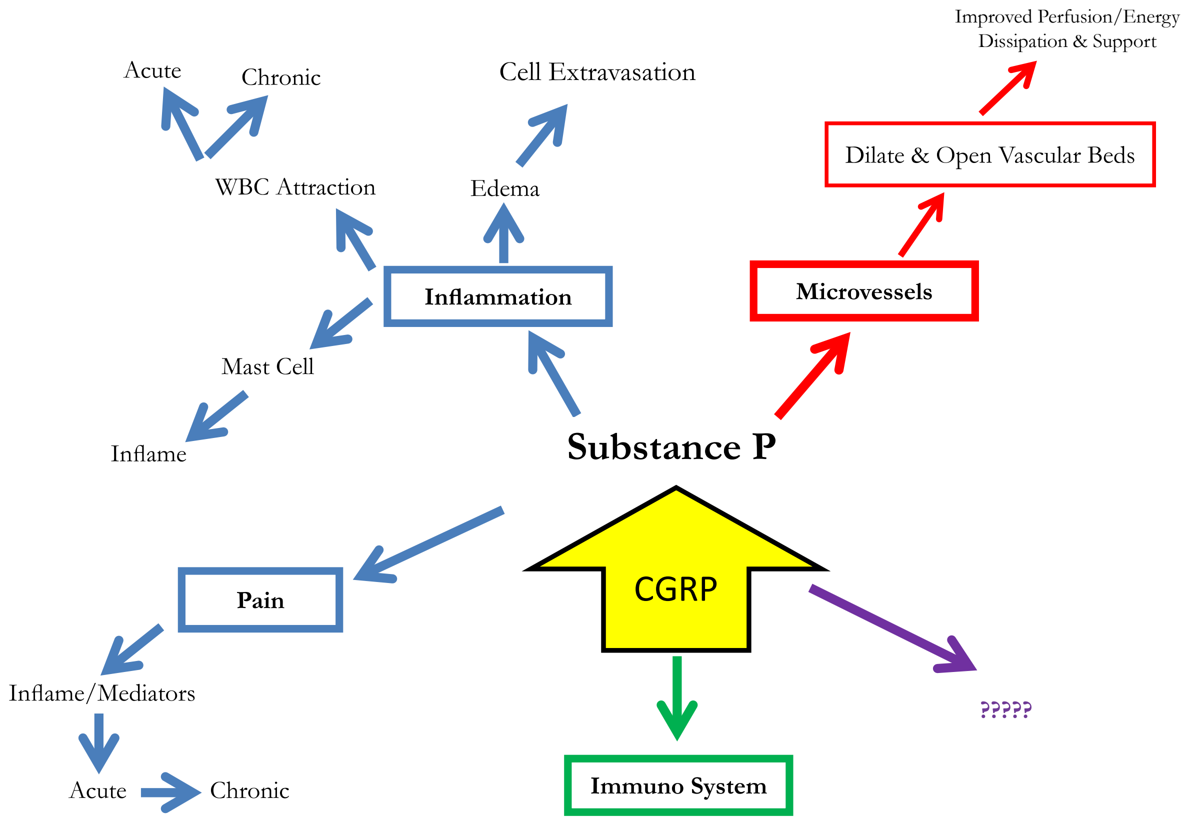


Figure 7: Schematic representation of potential effects of substance P (SP) and calcitonin gene-related peptide (CGRP) when they are released into the tissues within the horse's foot. Under most normal conditions, SP appears to promote vasodilatation of the microvessels when the solar surface of the foot is activated either by tactile/ light pressure or perhaps even vibratory stimuli (RED), such as when on a conformable surface. Released SP binds to tachykinin receptors on the endothelial lining of microvessels in the palmar foot, causing the release of nitric oxide (NO). The small molecule NO has potent effect on small vessels in dilating them to provide cushion support for caudal foot, energy dissipation, and for increased perfusion of the foot—at least when compared to horses standing on a hard surface. At other times, these neurotransmitters can promote the health and well-being of the immunosystem by increasing the manufacture of supportive proteins, immunoglobulins, etc (GREEN).

Much is known regarding the combined release of SP and CGRP from the sensory terminals in tissues and their relationship to the inflammatory response (BLUE). Usually an offending stimulus causes the release with these peptides promoting the attraction of white blood cells and their anti-inflammatory processes (phagocytosis, edema formation with protein and cellular extravasation through the vascular linings, etc.), or mast cells which can release histamine into the tissues promoting further inflammatory reactions. While these effects are occurring within the tissues, the nerve fiber electrical activity is coursing to the spinal cord and brain for local reflex changes as well as the perception of painful stimuli. With long-term effects, the pain becomes chronic and the individual nerve cells in the spinal cord and brainstem become very sensitive to the same or similar stimulus (usually referred to as "wind-up"). These possible effects within the tissues have been studied in many animals previously, and are most likely occurring in the horse's foot. Other effects of the released neurochemicals are being examined by many research scientists around the world (PURPLE, undiscovered). Robert Bowker files.

Chemically-Identified Nerves Within the Foot

Now that we have introduced the three basic types of sensory receptors and the fact that there are numerous neurotransmitters being released from sensory nerves, the question is what do they do—either in general way, or in a more specific sort of way?

Within the horse's foot, these released chemicals have significant effects upon (1) the horse's internal foot tissues, (2) the various vascular beds within the foot and (3) the horse's perception of ground surfaces. When these neurotransmitters are released from the sensory nerves into the peripheral tissues, they trigger different events, depending upon what the neurochemicals are, where the neurochemicals are released from the sensory nerve terminal, and on what cell types/receptors the neurochemicals come into contact with. Each effect upon the tissue will also be dependent upon what other neurochemicals released from other nearby sensory nerves, as these neurotransmitters will enhance, lengthen or perhaps shorten the effective time period of neurochenical actions. These events include generating action potentials, prolonging the effects of other neurotransmitters at their sites of action, affecting the vasculature in terms or blood flow and tissue perfusion, recruiting other cells/immune system mediators to the site to promote healing mechanisms, and/or having even negative effects with chronic neurotransmitter release within the horse's foot.

The list is almost endless as to what these sensory neurotransmitters promote within the horse's foot tissues. What we are trying to say is that these many thinly myelinated sensory nerves will actually provide a "motor effect" within the tissues. This concept of tissue effects in the periphery by the sensory nerves was not known until the early to mid-eighties when scientists[33,38, 24,58] discovered that activation of the sensory nerves actually released chemicals peripherally into the tissues from the nerve fibers, in addition to conveying the "sensory information" to the spinal cord. This concept represented the major change in our way of thinking about sensory nerves as not being exclusively conveying information **towards** the spinal cord and brain from the periphery. Rather, these profound effects seen in the peripheral tissues by the nervous system indicate that the neurochemicals released into the tissues from the sensory nerves can influence the outcome of the disease process: they can ameliorate and contribute to the healing process, or these same neurochemicals can also exacerbate the healing process, as in chronic diseases (Figure 7).

Sensory Effects

The following example illustrates that two very similarly shaped objects can evoke two different sensory effects and form different perceptions: a primary sensory effect of touch with the information passing to the brain or several effects where the same sensory nerves can convey tactile information to the brain as well as evoking significant "motor-like effects" in the periphery. In this example, when we place similarly shaped and size fruits in our mouths: a cherry and a jalapeño pepper, the effects are very noticeably different. These two pieces of fruit will activate different nerves. The sensory information from the cherry will activate touch receptors in our cheeks and tongue and proprioceptive receptors around tastes buds, tongue muscles and fibers as well as our teeth. When we bite into the cherry we will also activate additional tactile and thermal sensory receptors as well as taste receptors, as we begin to appreciate the sweet or bitter taste of the cherry, as well as its physical features via the tactile and mechanosensitive receptors and fibers. These and other effects that we perceive are usually carried out by the mechanosenstive receptors and their nerves as we begin to perceive an increase in salivation.

On the other hand, when we place a small round jalapeño pepper in our mouths, we can also activate these same taste, tactile and proprioceptive receptors and nerve fibers as we appreciate the pepper's physical features. However, there are some other changes that we will become aware of as soon as we bite into the pepper, which will be somewhat different than that of the small cherry. The opening of the jalapeño pepper also releases a chemical called capsacin, into our mouths. The chemical capsacin will specifically activate the many thinly myelinated or naked sensory nerve fibers, which will release Substance P (SP) into our mouths. This release of SP from the sensory nerves will have a cascading effect to affect other nerve receptors within our mouth as we begin to "appreciate" the burning sensation on all mouth tissues that have come in contact with the capsacin from the jalapeño pepper. These other sensations will include pain and perhaps burning sensations along with a warming and reddening effect of the inside of our mouths. The pain and possible edema effects are due to the thinly myelinated nerve fibers being activated with the release of SP from the sensory nerve terminals, which will also dilate the superficial blood vessels lining the mouth through the activation of the NK1 receptors on blood vessels. These vascular effects will produce a warming sensation as more and more blood flow occurs through the dilated vessels and our cheeks will become reddened with this increased blood flow through them. If the peppers are hot enough to release large quantities of capsacin-like ingredients, then even edema may occur locally in our mouths as the spaces between the cells lining the vessels allow fluids to leak into the interstitial spaces.

If the reaction is severe enough, then an inflammatory reaction is produced by the SP release into the tissues with the attraction of white blood cells and other inflammatory agents. These effects within our mouths are just an example of how similar objects can activate different sensory nerve fiber types with totally different effects within our body tissues depending upon which of the neurochemical agents that are released from the sensory nerves. Other common examples of the effects of SP include pepper spray that many people use as defensive protection of their own person and capsacin hand cream that many people use to decrease the arthritis pain in the joints of their hands, etc. Both seem to act via the release of SP from the sensory nerves in our corneas or in our joints, respectively. Finally, when SP is released alone from a sensory nerve terminal into a tissue region, it may have an effect for a microsecond or so. However, if another chemical is also released with the SP then the effects of SP are prolonged for 5-7 seconds, which is an "eternity" in terms of neurotransmitter effects (Figure 7). Such an effect may be important in more chronic situations when the sensory nerves are apparently releasing these neurochemicals into the tissues for extended time periods.

Tachykinins

One such group of pharmacological receptors known to be present on the vessels within the horse's foot are the tachykinins.[15,55,56] This is a group of receptors that have similar pharmacological properties that carry out their "drug actions" by SP-related compounds. There are three pharmacological types of this receptor named neurokinin 1 (NK1), NK 2 and NK3.[36,47] Substance P (SP) binds preferentially to the NK1 receptors and does not bind (or binds very little) to the other two types, while if you modify the SP protein (eleven amino acids) and just change one or two of them, the "drug actions" will change slightly to increase or decrease how active the SP-like compound is. When SP is released from sensory nerve fibers and it diffuses to the vasculature it is a potent vasodilator in most horse tissues. (NOTE: this above is an example of the same neurochemical being released, but activating different receptors depending upon the location of the neurochemical and being coupled with a pharmacological receptor.)

When NK1 receptors are activated, the SP binds to the NK1 receptors much like a "lock and key" mechanism. The microvessels respond by dilating, as the cells along the inside of the blood vessels called the endothelium release nitric oxide,[26-28] which induces smooth muscle relaxation of the microvessels. Such an effect upon any vascular bed will increase the diameter of these very small vessels and enhance the perfusion of the tissue, as greater numbers of vessels become available for blood flow. When we modify the amino acid arrangement of the origin SP protein, the "modified SP" may affect other types of receptors in tissues but they will be less likely to be able to bind to the SP receptors on the vessels to cause dilatation. This "modified SP" has a new "shape" to it, and as a result of the change in shape, it will not serve as a "key" to fit into the "lock and key" mechanism of the original SP receptor very well.

Perceived Sensations and their Physiological Changes:

Pain sensory receptors and nerves:

With the sensory nerve fibers, a variety of neuropeptides have been identified to be present in these thin myelinated nerves with SP and calcitonin gene-related peptide (CGRP)—being the most studied concerning pain. These two nerve neurochemicals present in the horse's foot usually co-exist in the same nerve fiber, which results in both neurochemicals being released simultaneously from the nerve terminals when pain sensation is activated, such as with a nail or wire penetration.[45] (Figure 8). The majority of the SP peptide within sensory nerves is concentrated peripherally in the tissues with about 75-85% of it being present in nerve terminals, while a much smaller proportion is located in the terminations in the dorsal horn of spinal cord itself. This aspect of the neuroanatomy of the chemically-identified sensory nerves having a peripheral concentration of the peptides, rather than having them concentrated centrally, has clinical implications during both normal and diseased conditions, as mentioned above.

Within the foot, whenever a painful stimulus is encountered, the induced neural activity is conducted towards the central nervous system, which activates multisynaptic ("Multi"—many; "synaptic"—location on the nerve fiber where nerve cells communicate with each other.) pathways in the spinal cord that are important for both local protective reflex mechanisms and more distant sensory perception.[58-60] (NOTE: Concerning the nervous system, when a multisynaptic pathway is activated, it means that the recruited nerve cells are attempting to protect the organism from the offending pain stimulus to minimize tissue damage and/or painful sensations. These now activated pathways are trying to withdraw the limb away from the stimulus and promote the inflammation physiological processes to try to stop the invading insult from further injury and to begin the healing process if possible.) This complicated process simply tells the animal that the painful stimulus hurts, but also in the periphery, due to the release of these neuroactive agents into the tissues, the physiology of the local tissue is altered: tissue perfusion can change as inflammation occurs, which is usually beneficial as a protective measure against the invading threat. Within the tissues a series of involved and

Tissue environment surrounding sensory nerve ending

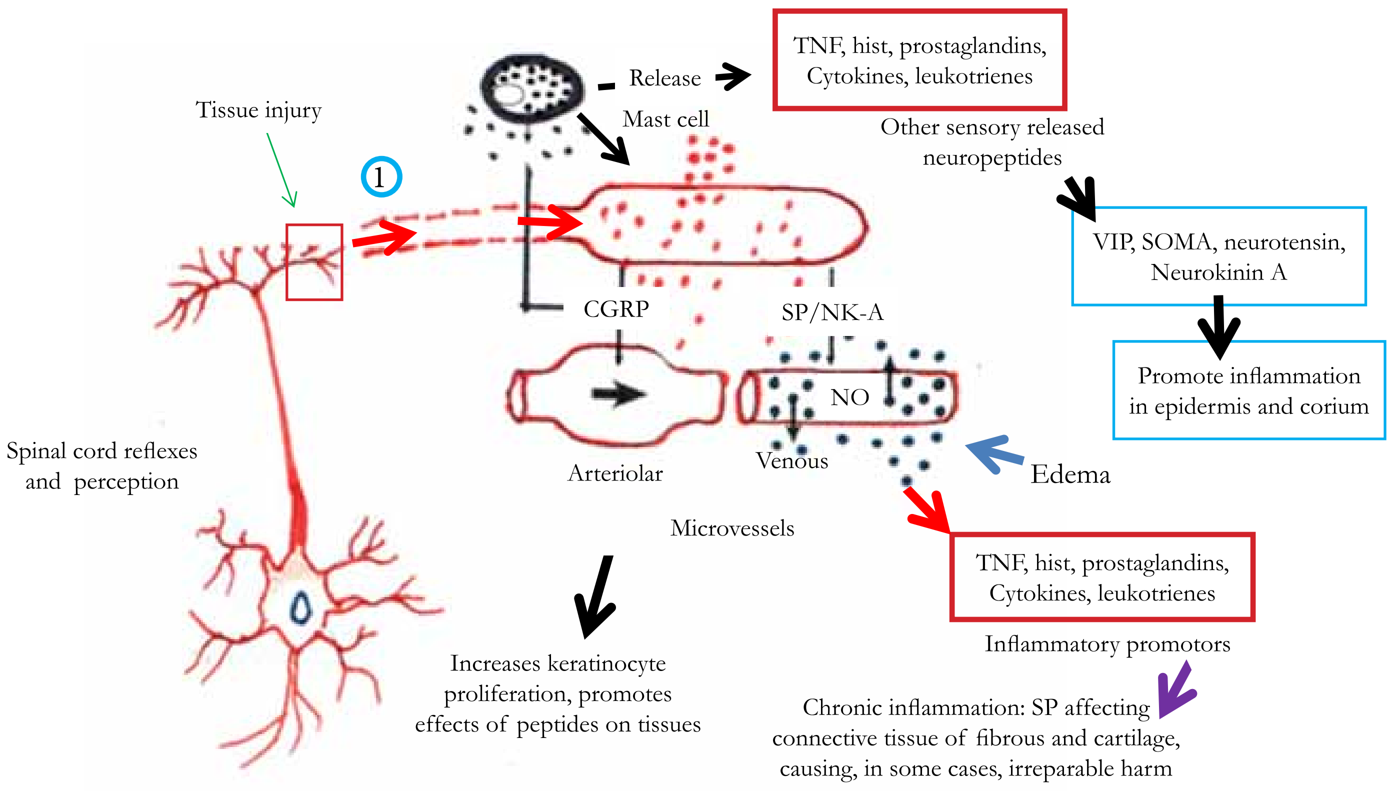


Figure 8: Schematic illustration showing the potential effects of SP and CGRP released from a sensory nerve terminal. Initially, a tissue injury (i.e. nail, stone etc) (thin Green arrow) occurs, resulting in painful sensation being conducted to the spinal cord (thick Green arrow) for incorporation into spinal reflexes (limb withdrawal) and perception by the brain. Within the environment surrounding the sensory nerve ending, the injury results in release of peptidegic neurotransmitters (RED dots), including substance P (SP) and calcitonin gene-related peptide (CGRP), into the surrounding tissues. When SP is released, it can act on specific receptors on the endothelium of venous microvessels to promote dilation via a nitric oxide (NO) release method; the receptors are called tachykinin receptors and are distributed throughout the horse's foot in association with microvessels. In addition, SP may also increase the "leakiness" of the microvessels causing edema formation (yellow arrow). This process of dilation and leaking of intravascular proteins and pro-inflammatory agents result in the inflammation present within the horse's foot tissues.

These effects include the release of tumor necrosis factor (TNF), histamine (hist) release from mast cells, and other immunopromoters (prostaglandins, leukotrienes, several cytokines, to name but a few. SP recruits white blood cells to the site of the neurotransmitter release, attracting neurotrophils and mast cells, enhancing/controlling inflammation and infections and allergic reactions, respectively. Each of the inflammatory promoters will enhance and prolong the inflammatory reaction within the tissues. Traditional treatments attempt to reduce/minimize the effects of foreign agent (bacteria) through the use of antibiotics or the inflammatory effects via the use of anti-inflammatory drugs. With chronic bathing of the tissue environment within these neuroactive and inflammatory promoters, the connective tissues become negatively affected as the fibrous and cartilage tissues may become irreparably damaged by the effects of these neuroactive agents.

A second and major sensory neuropeptide released from sensory nerve terminals with the insult, includes CGRP, which is usually localized in the same nerve terminal with SP peptides. CGRP promotes SP in that it prolongs the effects of SP when it is released into the tissues by decreasing its rate of degradation. This effect may have a negative impact on the healing and recovery of tissues, as it may prolong the inflammatory effects. Within the epidermal tissues CGRP promotes vasodilatation of the arteriolar micorvessels, as well as has more direct effects upon keratinocytes by increasing their proliferation. Several other neuropeptides have been identified within the horse's foot and include vasoactive intestinal peptide (VIP), somatostatin (SOMA), neurotensin and neurokinin A (NKA). All of these chemicals are present in the sensory nerves and are presumably released into the tissues of the horse's foot when they are activated either by direct injury or perhaps even a non-penetrating injury to the tissues, or even a more indirect method through the facilitated release by SP or CGRP. These effects by the sensory nerves appear to be very significant in promoting the inflammatory disease, whether the inflammatory process is acute or more chronic. In either instance treatments of the disease processes will usually involve being aware of the effects of the sensory nerves.

complicated events occur with the activation of the immune system and inflammatory processes: a series of cascading molecular events and processes occur with the invasion and release of different neurochemicals and other molecules into the affected site. All of these now-active processes are geared towards protecting the organism and promoting healing. When these two neurchemicals- SP and CGRP (calcitonin gene-related peptide) are released together from the same nerve fiber into the tissue, the duration of the inflammatory effects are prolonged by increasing the half-life of SP,[36,39,40,51-53] as we have mentioned previously. This inflammatory reaction promotes the attraction of white blood cells, and the NK1 receptors are activated by these neurochemicals on vessels to cause vasodilation and erythema (reddening of the surrounding tissues). These two processes further induce edema formation, and promote the release of additional inflammatory agents from cells (Figure 8). With the activation of the NK1 receptors by SP the dilation of the vasculature represents a potent effect of SP, which occurs via nitric oxide. These inflammatory effects, with the release of SP into the periphery, can be abolished when these sensory nerves are cut or ligated. [33, 36] These lessened inflammatory effects will often be seen in horses with surgical neurectomies, further supporting the notion of sensory nerve activation in promoting inflammatory responses. In chronically inflamed tissues, these neurochemicals have been shown to increase in the tissues (as occurs with rheumatoid arthritis in humans) and begin to degrade the actual integrity of the connective tissue elements.[36] We believe that in the horse, the more chronic a disease or problem becomes, such as with chronic laminitis, the more likely that these same neurochemicals will have deleterious effects upon the integrity of the tissues.

Thermal receptors and nerves:

These types of receptors respond to temperature, primarily within the innocuous range—as beyond this range, body tissues begin to be destroyed, activating the pain-sensitive fibers. The potential presence of thermal receptors in the horse's foot is supported mainly from anecdotal observations in different behavioral situations, such as when a horse resists moving on hot surfaces or in deep snow and ice, while the internal foot tissues remaining viable under these extreme conditions. The horse appears to be less affected with the cold surfaces, although these cold surfaces may not be extreme in temperature. The physiological evidence that the tissues respond to temperatures has been obtained from recordings using thermal probes in the horses feet during cold periods.[46] The temperature fluctuations are believed to be due to the opening and closing of arteriovenous anastomoses (AVA) within the dermis of the hoof wall.[31, 43] Functionally they appear to be the same that we have in our own fingers.[31] Interestingly, there is a physiological difference between the two nerve

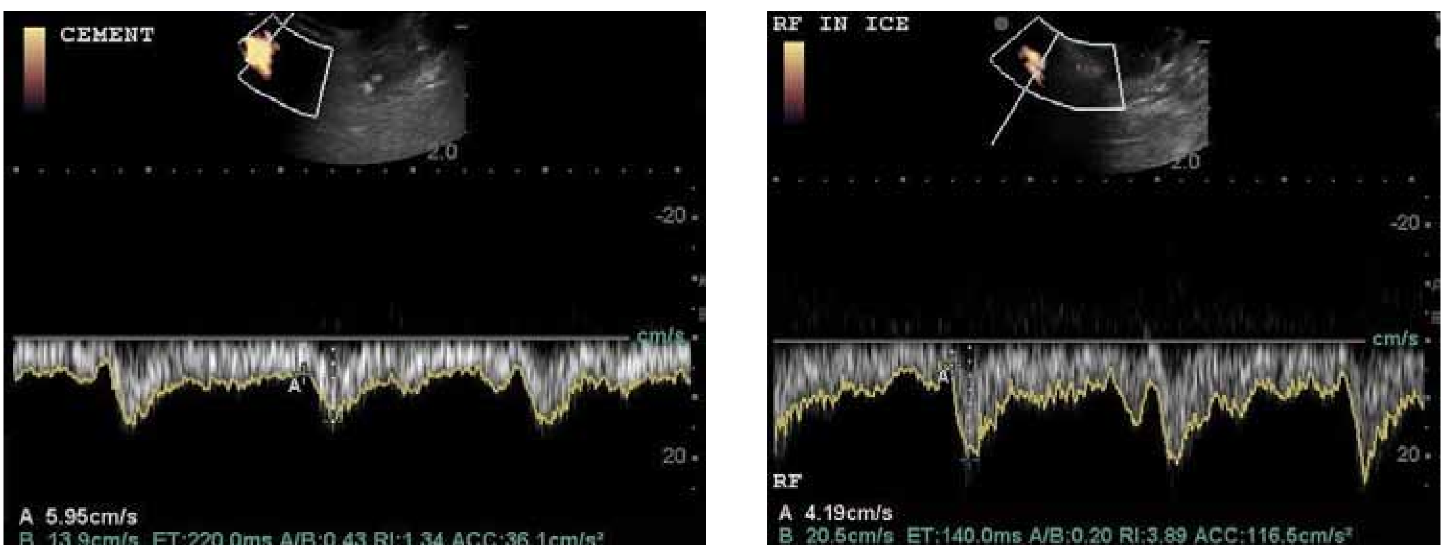


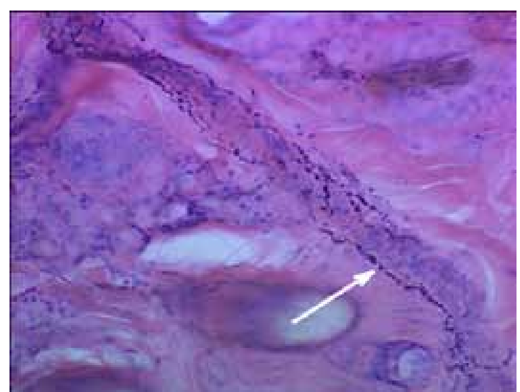
Figure 9A (left): In this example [methods described in detail later in this chapter], the venous blood flow at the level of the fetlock was measured showing a normal waveform that pulsates (arrows)-wave acceleration (speed of waveform to reach peak velocity) is slower in the normal recordings (acc: 36.1 cm/s) and the sensory nerves appeared affect the flow as the waveform becomes more sharply defined when foot placed in cold water (9B right) before there was a any change in flow due to cooling of the foot. Within a few minutes the venous flow changed as evident by the increased acceleration of the venous flow. These changes occur very rapidly and appear to be due to nervous activity due to thermal changes as the blood flow did not appear to change. This direct evidence of sensory nerves affecting flow is preliminary; however, more conclusive evidence of the sensory nerves having a direct effect in flow is seen during recordings of blood flow in the opposite, but not cooled, limb (see below Figure 21A and 21B later in this chapter). In this instance the sensory nerves conduct thermal information from the iced forelimb foot to the opposite limb and result in a similar decreased perfusion of blood through the foot. Robert Bowker files.

types in the firing frequencies and response capabilities, as well as structural differences of these nerve fibers within the tissues.[19, 22] Cold temperatures do appear to have both a direct effect upon the vasculature within the foot, as well as an indirect effect via activation of sensory nerves innervating other body areas. In figure 9, a fairly rapid and more direct effect can be seen by having a horse place the foot to a level below the coronet in cold water and recording the blood flow exiting the foot. While many of these thermal receptors respond to only temperature changes in the superficial surfaces, there are some thermoreceptors (termed polymodal) that respond to various stimuli besides temperature, such as when certain chemicals are applied to the skin surface. These observations indicate that there is a dynamic, but complicated relationship between thermal receptors and other types of sensory receptors. There can be a specific sensory stimulus, which can differ from a specific chemical stimulus. In any event, both anecdotal and physiological evidence supports the idea that there are thermal receptors in the horse's foot and the horse can perceive the temperature differences in hot and cold ground surfaces.

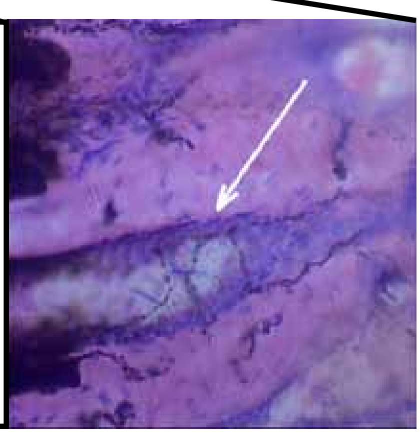
Clinical and physiological significance:

The activation of these pain-conducting nerves can produce effects both in the spinal cord and brain, as well as in the peripheral tissues. Pain sensation is a potent input that dominates most reflex responses, as the organism attempts to protect itself from further injury. Peripherally in the tissues, substance P and other neurochemicals are related to the inflammatory processes when they are released from the sensory nerves, as we have described above. It is these events that most clinicians deal with during a lameness examination, as the perineural or synovial deposition of the local anesthetic will help desensitize this painful region within the foot for the localization of the lameness issue. In chronic instances, the sensitivities and inflammatory effects within the tissues may be exaggerated (as compared to normal) due to the continuous release of these neurotransmitters into the tissues.[36] In these instances, usually referred to as "wind-up", any ever-so-slight stimulus will set off an intense response of pain sensation that is well beyond the same stimulus produced under normal conditions.

Figure 10A: Schematic figure showing nerve fibers (RED) wrapping themselves around the hair follicles in the coronet. These are tactile mechanosensitive nerve fibers, as well as movement-sensitive and pain or nociceptive nerve fibers. These nerves are very sensitive to any slight bending of the hair shaft or possible indenting of the skin that moves the hair. Any insect landing upon the hair shaft or movement of the skin over the coronet will most likely discharge the nerve receptors for producing electrical activity to be transmitted to the spinal cord. These same peptide-containing nerve fibers can also be seen to pass into the basal layers of the epidermis overlying the corium of the skin. Robert Bowker files.



In figure 10B, using immunochemical techniques, sensory nerves fibers can be seen to wrap themselves along the hair follicle (white arrow) towards the surface of the skin. These sensory nerves, identified as CGRP containing fibers, will be responsive to physical deformations of the skin and hair follicle and to painfully applied stimuli. Robert Bowker files.



In figure 10C, the Substance P-like neurochemical—neurokinin A—innervates the small vasculature associated with the skin overlying the coronet. Neurokinin A is a small peptide released from the sensory nerves that can promote vasodilatation of the microvessels in the skin, which causes increased warmth and reddening (erythema) along with other potentially pathological effects.

Types of Mechanoreceptors in the Equine Foot

In addition to the sensory nerves for pain and thermal transmission, there is another group of receptors ranging in complexity from free nerve endings to specialized complexes that convey other sensations, ranging from light touch to pressure and vibration: these sensory receptors are called mechanoreceptors, as the induction of the nerve electrical activity is due to physical deformation of the receptors by an environmental stimulus rather than actual destruction of tissue.

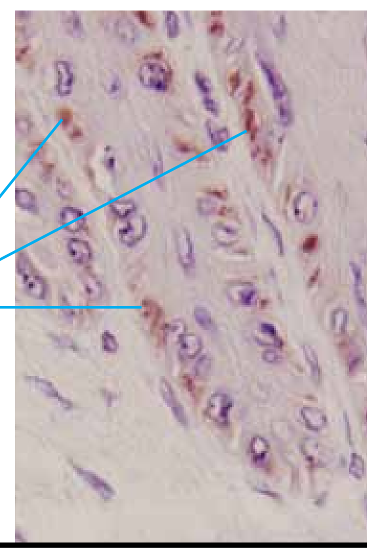
Mechanoreceptors identified in equine feet convey sensations of touch, pressure, and vibration. These mechanoreceptors are important to a horse's everyday activities that involve standing and moving. Touch receptors in the feet work in combination with proprioceptors in muscles, tendons, ligaments and joint capsules. The combined input into the central nervous system is part of the unconscious reflex system. It enables all flexor and extensor muscles around each of the joints in the forelimb to contract, permitting normal stance during relaxed posture, as well as the correct sequence of muscular contractions and joint and limb movements during walking and trotting etc. Which specific mechanoreceptors are activated depend on which foot structures are loaded at any given time. This will, of course, vary with changes in hoof balance, shoeing, and ground surface.

Although touch, light pressure and vibration are often classified as different sensations, they are all detected by similarly-constructed sensory receptors that are activated by mechanical or physical stimuli. There are generally three categories of these mechanoreceptors. The first category reacts to the sensation **of light cutaneous contact or touch** which usually deforms these receptors located superficially in the epidermis and dermis of the coronet or the dermis of the frog, and perhaps of the hoof wall; these receptors can range from free nerve endings to specialized receptors. Touch and light pressure are difficult to distinguish electrophysiologically, as when one performs one stimulus, the other stimulus is also activated simultaneously. Thus they are often classified as similar sensations.

The second category senses **deep pressure**. This pressure sensation is detected when a greater physical force applied to the skin and foot to deform the deeper tissues of the dermis, such as that applied when the foot tissues are fully loaded during stance or movement.

The third category of receptors perceives **vibration sensations**. These receptors are activated by the rapidly applied physical stimuli of ground impact or shifting posture. Together these various sensations are fed into the nervous system for incorporation into the centrally programmed reflexes and movement patterns, which enable the horse to move and perform as an athlete. In addition to the impact energies created by the fully loaded foot and the ground, other vibrational energies are perceived as energy waves, and are transmitted through the ground and detected by the foot when the horse is standing.

Figure 10D schematically shows the locations of Merkel cells within the basal layers of the epidermal tissues of the foot or along the boundary between the epidermal and dermal regions. The Merkel cells are nestled among the keratinocytes and other cellular elements of the epidermis. These cells are slowly adapting, meaning that when activated they remain firing and responding to the stimulus as long as the stimulus is being applied. An example is when the solar surface of the foot is touched or comes into comes into contact with a ground surface, especially a conformable surface. Meissner's corpuscle may also be present within the epidermis of the horse's foot particularly the frog region as we have seen a few structures resembling these sensitive touch receptors. Future works will have to resolve this very interesting question.



In figure 10E, an immunochemically stained slide shows Merkel-like cells in the basal layer of the epidermis of the SEL from the hoof wall. These stained cells identify the locations of these types of tactile/light pressure cells of the equine foot. Robert Bowker files.

The following is a brief outline of the types of mechanoreceptors within the digit of the horse (Figure 10) and the main sensations they respond to:

- Free nerve endings are sensitive to touch and pressure. They are situated between epidermal cells and have a similar structure to the free nerve endings that provide temperature or pain sensations.
- Merkel's discs are fine touch and light pressure sensitive neurons located in the lower epidermal layer of the skin and hoof structures.
- Meissner's corpuscles are fine touch and pressure receptors located in the dermal tissues.
- Pacinian corpuscles are large receptors, sensitive to deep pressure, pulses or low-frequency vibrations in palmar dermis and surrounding secondary DDFT insertions.
- Ruffini corpuscles are located in the dermis of the skin and are associated with the neurovascular bundles along the pastern. They are sensitive to pressure and distortions, or stretching of the skin and hoof.
- Root hair plexus is made up of free nerve endings associated with the hair follicle around the coronet to detect subtle movements of hair.

Clinical Considerations

Equine veterinary medicine has traditionally not considered the sensations of touch or light or deep pressure receptors as being significant factors in assessing locomotion or movement during a physical examination of a horse. The veterinarian performing lameness examinations aims to determine if pain originates in the distal limb, using a variety of measures and tools. Such mechanical, but simple, tools as a hoof testers and knife or pick have been used in several creative ways provide sufficient information for the veterinarian to determine whether pain is present within the foot.

While hoof testers applied across the sole and wall are often used to detect pain, they usually can produce a deeper pressure sensation in the normal foot, similar to when the horse stands on an irregular ground surface. When the tissues are more inflamed and sensitive, a painful sensation may be perceived by the horse for similarly applied hoof tester pressure as the same stimulus will presumably activate the now irritable SP nerve fibers. The released SP into the tissues will produce many of the inflammatory effects that were mentioned above. If a painful interpretation is perceived by the veterinarian, they then try to localize a more precise source of that pain with perineurally or intrasynovially local anesthetic injections and then treat the potential problem. However from the horse's perspective the activation of the deep pressure, or the non-painful, receptors, may be more important than the perception of pain. These mechanoreceptors provide sensory information and sensations that the horse uses in their everyday lives to negotiate their environments as they interact with other horses and carry the rider.

Mechanoreceptors transmit information about the horse's environment that determines how the limbs should respond during movement and stance. This sensory information informs the horse's reflex and locomotor neural pathways as to how the fore and hind limbs should be coordinated, how long or short the next stride should be or how much the individual limb muscles should contract to carry out these limb movements or to maintain a stance posture, to name but a few. Normally different parts of the foot will be loaded during each of the different phases of limb stride from initial ground contact to the mid-stance position, and to the onset of break over. Further, in a lame horse, the normal sequence pattern of movement may potentially be altered, resulting in different receptors being activated and in different sequences. Other factors will potentially activate different receptors either in their "proper" sequence or preference, including the gait, locomotor speed, and trimming and/or shoeing variables, which may affect foot flight. These same sensory receptors will also inform the horse about the positions and tensions of the tendons, ligaments and joints prior to the next foot fall. This wealth of sensory information is acquired and processed in a brief moments time, allowing the neuromuscular structures to reflexively respond in a coordinated manner.

As the foot moves from initial ground contact through mid-stance to lift-off, different receptors are activated as different parts of the foot contact the ground (Figure 11).
If we can simplistically break down the movements of the foot through a step cycle into three phases, we might begin to appreciate the complexity of the neurosensory and neuromuscular events occurring within the distal limb of the horse. The three phases are (1) initial ground contact, followed by (2) a mid-stance phase and then (3) lift off of the foot.

Sensory information informs the horse's reflex and locomotor neural pathways as to how the fore and hind limbs should be coordinated, how long or short the next stride should be or how much the individual limb muscles should contract to carry out these limb movements or to maintain a stance posture, to name but a few.

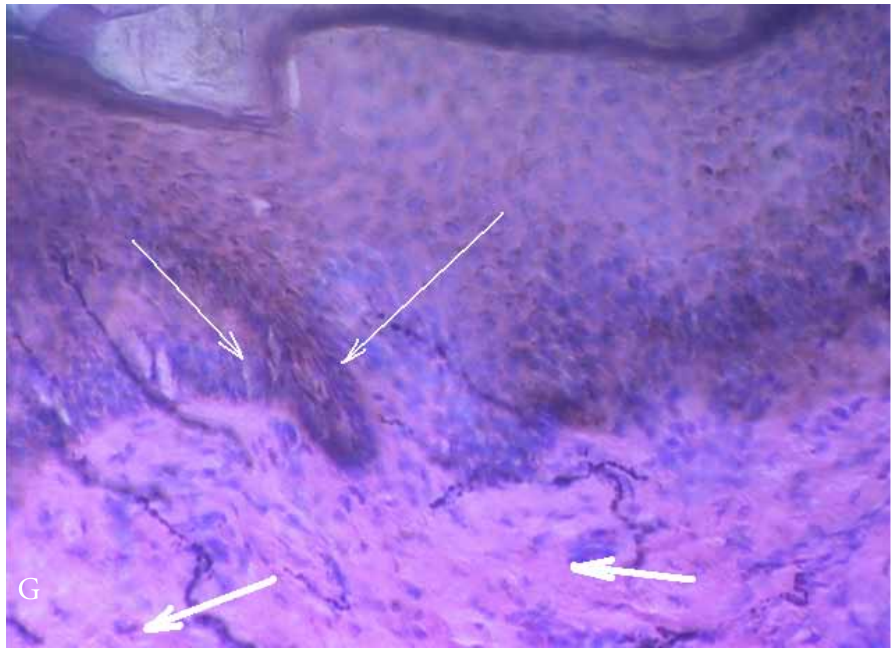
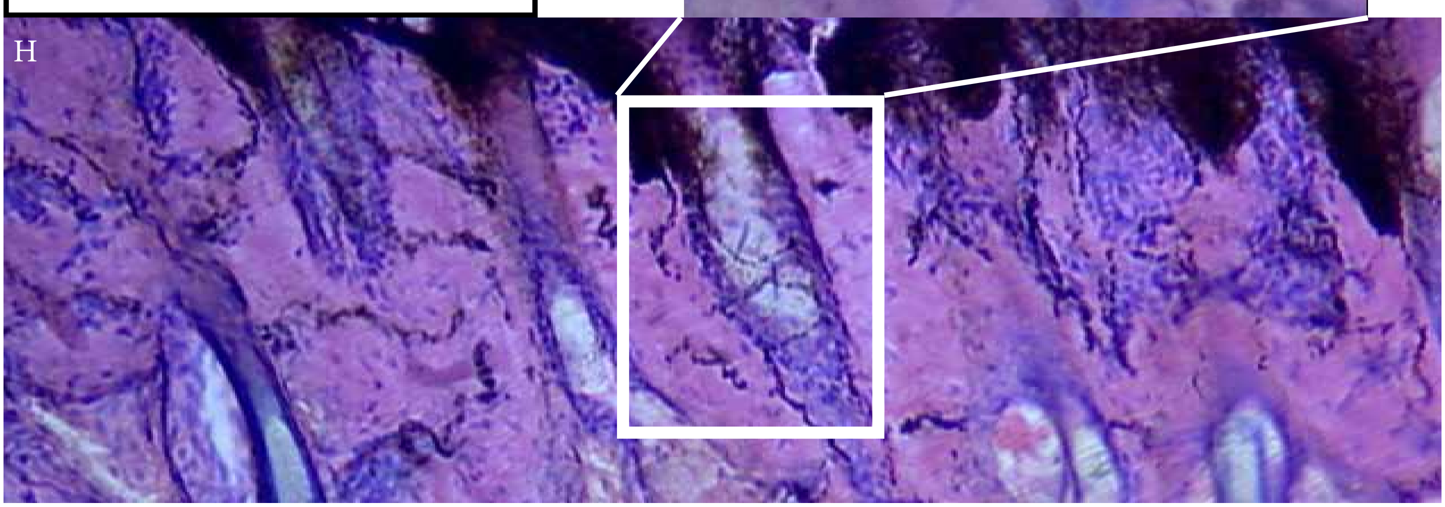
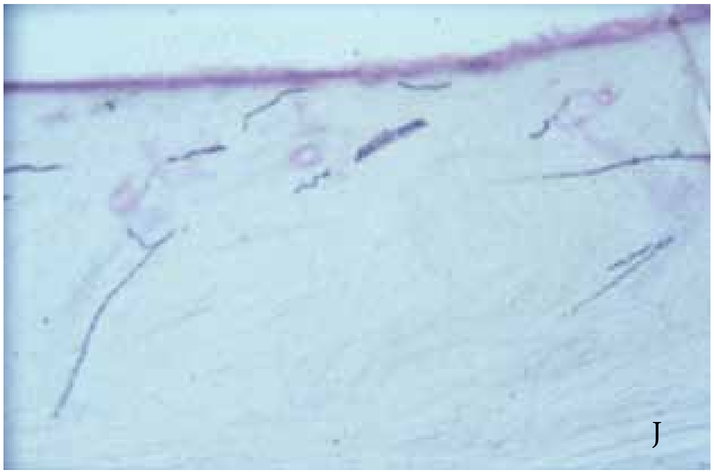
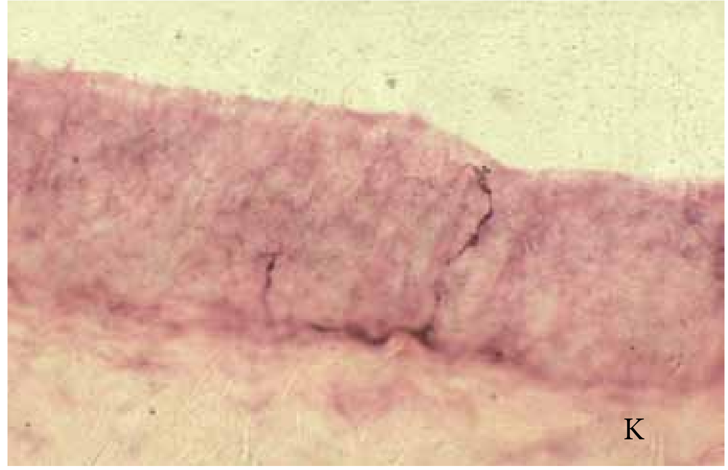


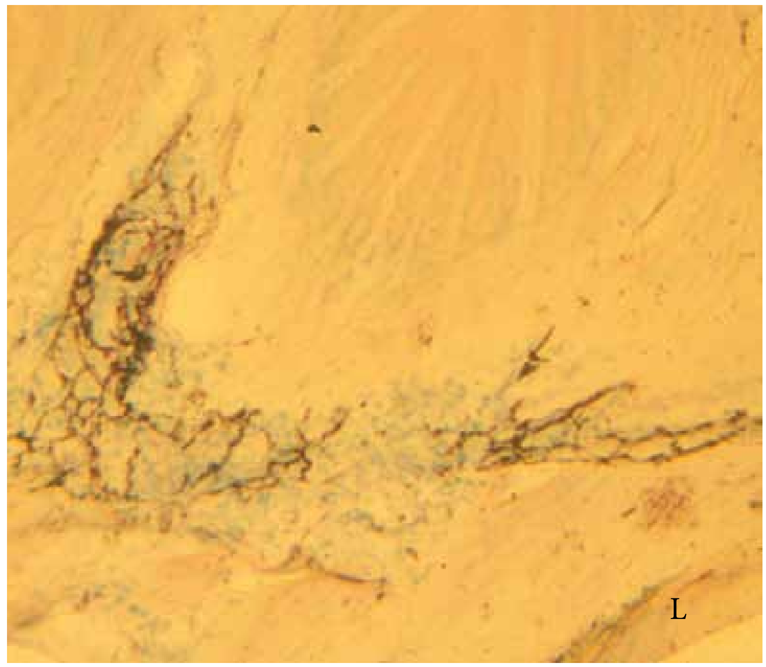
Figure 10F: Schematic drawing of free nerve endings present within the dermal (RED) and epidermal (BLUE) layers of the hairy skin of coronet (figure 10H), and hairless skin lip (figure 10G). These sensory nerves are present in all regions of the skin including the frog and hoof wall. They are responsible for sensory perception (pain, thermal -warmth and cold receptors- and likely tactile stimuli) and for mediating tissue effects of changing perfusion through the tissues and inflammatory response if needed. In these frozen histological sections, the sensory nerves are also distributed throughout the dermal tissues and through the basal layers of the epidermis. In fig 10H, the SP fibers surround the hair follicle (blocked area -arrow) and are shown in an enlarged figure in figure 10I. Within the corium sensory fibers of these unmyelinated nerves are also present throughout the dermal tissues (thick arrows in figure 10G). Robert Bowker files.

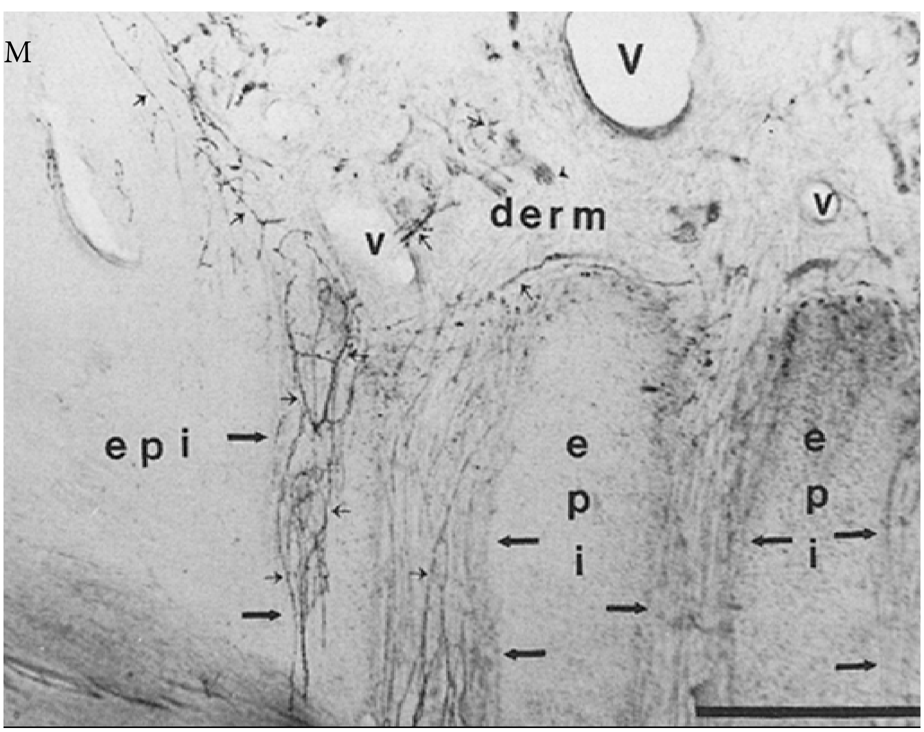






In figures J –M photomicrographs of these thinly myelinated peptidergic sensory fibers are present throughout the tissues of the foot, including the proximal suspensory ligament of the navicular bone (fig J), the synovial lining of the coffin joint (fig K), the dermal laminae (fig L) and the tubules of the dermal sole (with permission of Bowker et al, AVMA, 1993, vol. 54, 1840-1843). This wide distribution of these sensory peptides in both the epidermal and dermal tissues but also the connective tissues indicates the importance in the physiological functioning of these sensory nerves in the horse's foot, not only for sensory perception but also for neurovascular regulation. Robert Bowker files.





Admittedly, the three subdivisions of the step cycle and the hypothetical changes within the horse's foot are only approximate in terms of the sequencing. During the initial heel contact with the ground surfaces, touch receptors associated with the skin over the heels bulbs become stimulated, closely followed by the impact vibrational energies being detected by the Pacinian corpuscles located in the slightly deeper areas of this foot region. As the foot begins to be loaded and expands near the region of the coronet, deep pressure receptors and other Pacinian corpuscles located more deeply within the foot become activated. Presumably the internal foot stresses and pressures within the foot increase between the coffin bone, the palmar foot and the solar foot as the limb moves toward the stance phase and becomes more upright.

Simultaneously, a negative pressure occurs within the more central palmar foot,[15] which will provide a different internal stimulation of these and other receptors within the deeper foot tissues. These more deeply-located sensory receptors include the Pacinian corpuscles associated with the lateral cartilage, as the cartilage rotates outwards (abaxially-"away from the midline") along with activation of the pressure and tension receptors present in the solar corium, and the tension and pressure receptors present with the ligaments of the foot and the tendons of the distal limb.

With the latter structures, Golgi tendon organs and muscle spindles have been well documented to be present within the tendons (as well as ligaments) near their insertions onto bones and within muscles of most mammals, respectively. Although not discussed in the present chapter, these sensory receptors will, in all likelihood, be active during the impact and breakover of the horse's foot as it moves through the different phases of the step cycle.

Associated with the neurovascular bundle between the fetlock and distally deep within the foot are the Ruffini-like endings/receptors that respond to stretches and changes in pressure within the loose connective tissues of the distal limb. The sensory information is then conveyed rapidly to the spinal cord for reflex activation of muscles, as well as to the cerebellum for coordination of these sensory inputs with the motor control activation of the different limb muscles. Some information (touch/deep pressure sensations) is also conveyed to the higher brain centers for conscious perception. Thus, during hoof and foot loading, many different sensory receptors are activated in the superficial and deeper regions of the palmar and other regions of the foot, enabling the horse's nervous system to gain a wealth of information about each phase of the limb stride for movement and then react accordingly.

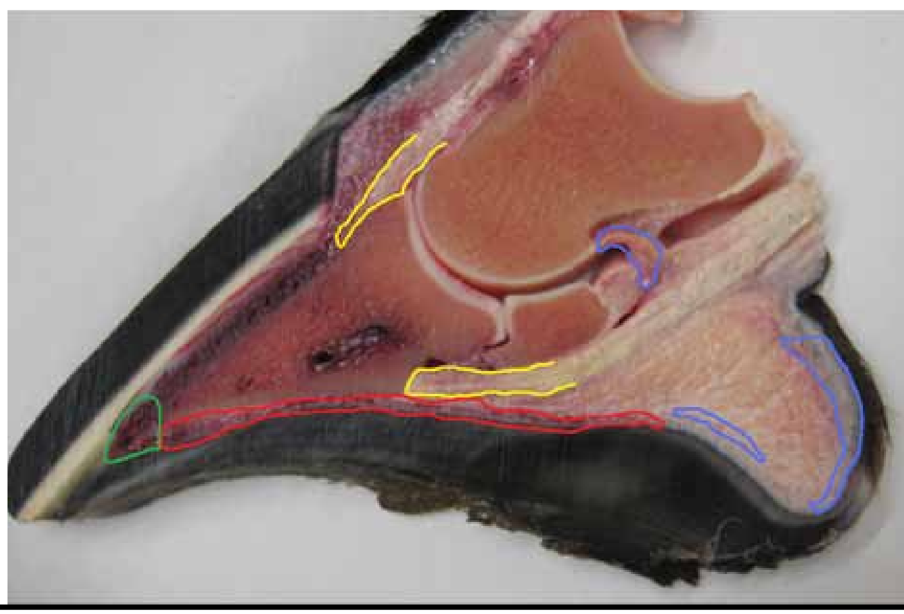


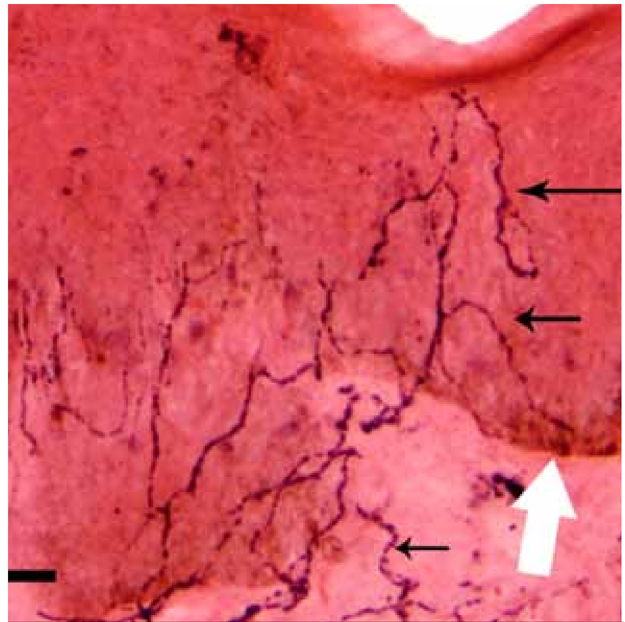
Figure 11: Photograph of the horse's foot showing the different foot areas where we have identified certain types of mechanoreceptors and what potential sequence they may be activated. Initially during heel contact, the sensory receptors of the palmar foot will be activated including the tactile and Pacinian corpuscles (Blue outline). As the distal limb begins to move towards the mid-stance phase, sensory receptors within the sole corium (tactile and pressure receptors) and in the tubules will become stimulated as the increased loading of the horse's weight is gradually achieved. Other Pacinian corpuscles, deep pressure and receptors associated with the ligaments and tendons will become more active than during the initial ground contact with the heel bulbs (Red outlined areas along the solar corium). Finally during breakover, as the foot leaves the ground, the pressure changes at the toe region (green area) will in all likelihood affect the sensory receptors within the corium of the toe as well as within the tubular dermis, as the foot transitions from a fully loaded structure to a non-weight bearing structure within a brief period of time depending upon the gait (Yellow outline indicates the DDFT and the extensor tendon inserting on the respective parts of the coffin bone). Robert Bowker files.

In addition to these above mentioned neuroactive processes, the ligaments surrounding each of the joint and synovial cavities between the fetlock and the coffin joint become a sensory resource for the distal limb during these same movements. Finally as the foot moves from the mid-stance phase and towards the termination of the step cycle, many of these sensory receptors will again be activated during breakover as the foot leaves the ground and becomes a non-weight-bearing structure. While this information will also contribute to the neurosensory and neuromuscular coordination complex of movement, we believe that this information and the sequence of inputs will be different than the events occurring during the initial phases of the step cycle. This hypothetical example merely illustrates that whenever an animal makes a step, the complexity of the sensory and motor responses is extraordinary and is well beyond most of our abilities to comprehend.

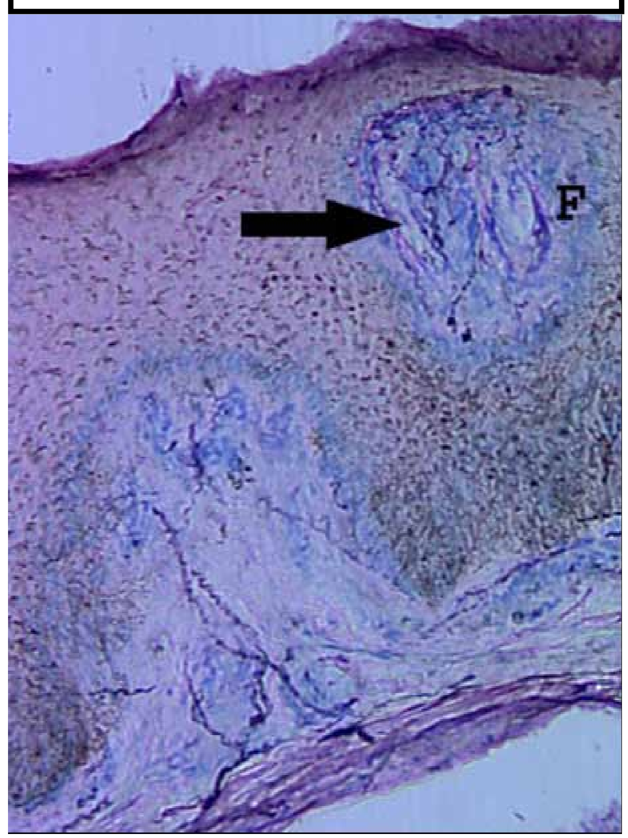
Free Nerve Endings — Merkels Discs:

Within the skin overlying the heel bulbs, many free nerve endings (Figure 12A and 12B) are present and can be seen to enter basal layers of the epidermis and extend towards the surface. These and other sensory nerves are distributed throughout the skin proximal to the hoof wall, including the coronet. They enable the detection of tactile/light pressure sensations applied to the skin above the coronet, and the superficial touches caused by insects, grasses, small sticks and other objects on the skin of the coronet, and hoof loading, as well as the thermal and pain sensations.

Some of these nerve endings surround the hair follicle or penetrate through the basal layers of the epidermis. When the hair shaft is bent, a deformation of the underlying hair follicle occurs which will stretch, bend or even flatten the sensory nerves innervating the hair follicle, resulting in an increase or decrease in nerve activity. The hair shaft can act to enhance the sensitivity of the sensory response of the nerves around the hair follicle.[17,42] Merkel-like cells are also present within the more basal layers of the skin and hoof wall. These cells were identified using immunochemistry to mark cellular particles peculiar to the Merkel cell. This cell is a slowly adapting receptor which responds to the detection of light touch and pressure sensations. The solar surface of the foot and the frog also appear to be sensitive to touch and light pressure sensations, as tactile stimulation will alter tissue perfusion (see below). This observation is very interesting as it suggests that the horse's foot, even though it is enclosed within a more hardened keratinized hoof, still appears to be able to sense and detect different sized particles and ground textures wherever the horse is standing. In other words the horse appears to be able to appreciate its own environment in precise detail.



In Figure 12A (above) the many very fine nerve fibers full of neurotransmitter SP can be seen through many of the layers of the skin. In Figure 12B (below), from the coronet, the hair follicle (F) entwined by these nerve fibers (arrow), suggesting that any bending of the hair shaft will produce a nerve activity. Interestingly placement of small "anklet" around the pastern of a horse will also stimulate the hair shafts resulting in a slight exaggeration of the limb movement. Robert Bowker files.



Pacinian Corpuscles:

During foot loading, the Pacinian corpuscles become activated providing critical information for movement (Figure 13A & B). The Pacinian corpuscles in the caudal foot are fairly large receptors (up to 1 millimeter in diameter) structured like an onion with many fluid-filled layers. This layered receptor responds to abrupt mechanical changes in the environment during movement. These mechanoreceptors are present in several locations of the caudal foot: (1) the superficial dermal tissues of the heel bulbs,[7,9,12] (2) the frog dermis surrounding the frog stay above the central sulcus,[9] (3) a few are scattered in the myxoid tissue between the lateral cartilage and the digital cushion and (4) a small cluster of elongated ones associated with the insertion of the DDFT onto the second phalanx.[12] These sensory receptors are situated in or near potentially critical regions when the foot initially makes contact with the ground surface, and they appear to be activated during all phases of the step cycle.

During locomotion these receptors respond to rapid tissue movement. They will be preferentially activated during caudal frog impacts, heel first landings, and when the lateral cartilages are forced outward (abaxially displaced), as well as when these structures are unloaded abruptly.[9, 20] *This positioning of the digital bones and the tightening of the DDFT and the secondary tendon during initial heel impact indicate that sensory information from the DDFT is obtained during virtually all phases of the step cycle: (1) during over-extension (dorsiflexion) of the hoof prior to heel contact when the major DDFT is extended, and (2) during coffin joint flexion when the major DDFT "relaxes" while the secondary tendon becomes taut, and during lift-off when the "elasticity" within the inferior check ligament aids in the pull of the DDFT and the distal bones of the limb.*

Prior to making contact with the ground surface, the foot normally will have a brief dorsiflexion of the pastern and coffin joints just before impact, which will provide a brief tension of the main tendon of the DDFT inserting upon the flexor cortex of the coffin bone. This abrupt extension of the distal limb joints, along with the outward expansion of the proximal foot and coronet during initial loading will activate the Pacinian corpuscles located at these regions of the foot. The elongated Pacinian corpuscles associated with the secondary tendon of the DDFT situated more proximally in the foot, must also be important at this initial stage of the gait cycle. After initial ground contact and flexion of the coffin joint, the distal end of the middle phalanx flexes towards the ground to actually pull the secondary tendon taut, even though the large DDFT appears to be relaxing.

These Pacinian corpuscles can respond to rapid changes in velocity and acceleration/deceleration of the distal limb joints in preparation for loading, as well as after the foot impact and loading of the foot. Pacinian corpuscles, by being rapidly-adapting receptors, respond to repeated *on and off* stimuli, such as those being applied during each foot fall. This abrupt *on and off* activity ceases to respond when stimuli are applied continuously, such as during continuous deformation of the receptor during stance. Abrupt pressure changes within the foot and in Pacinian corpuscles during foot impact, compress the fluid filled layers of the receptors to initiate an action potential, and this information passes to the spinal cord to be subsequently incorporated into limb reflexes during movements. This sensory information is critical to the horse, as it provides the afferent or sensory information from the feet and limbs to the centrally programmed generator (CPG) of locomotion within the spinal cord. The CPG produces the automatic or rhythmic oscillations of movement-related cells in the spinal cord, enabling flexor and extensor muscles of the limbs and back to function in unison and reciprocally in a reflex manner. The CPG of the horse does these complicated switching processes from the flexor to the extensor muscles with little effort and without conscious thought as the horse moves at different speeds across varying ground surfaces with an accomplished rider on their backs. During these shifts in speeds and lead changes, and the like, the CPG permits the coordination between all four limbs and the rest of the body, including the head, neck and back. In other words, the CPG enable us—both humans and horses—to run without thinking, and this activity of the CPG in coordinating sensory information from the periphery with the muscular activity is critical to our "normal" gaits.

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The complexity of the neural mechanisms underlying the CPG's generation of these *simple* limb coordination processes and how the CPG's activity changes almost unconsciously are mind boggling and difficult for us to appreciate. However, we can begin to appreciate what the CPG accomplishes during movements if you can imagine yourself jogging along a wooded trail during your afternoon workout. During this jog your arms and legs would be moving in an identical locomotor pattern as they will be coordinated with your back and neck movements as you move over the irregular surface of the forest path. Now imagine if you placed a small 30 pound sack on your back to simulate a rider as you jogged along this same path. You can begin to appreciate the neurological changes occurring in your leg and back musculature as these same muscles are still performing as you jog along the path but now with greater muscular effort as your legs and back must support an additional 30 pounds. The added sensory feed-back from your feet and muscles is due to the greater weight being placed upon the joints and limbs and this feeds into the CPG to produce a coordinated muscular effort. The CPG does all of the internal spinal cord changes with little effort.

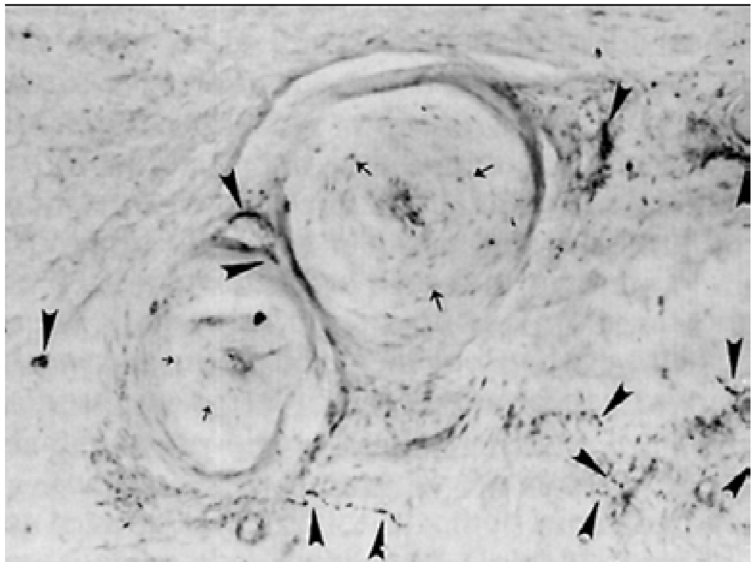


Figure A: Moderately high power view showing Pacinian corpuscles in the heel bulbs of the caudal foot. These large spheres with a centrally-lying nerve axon can be seen. Among the round receptors are small nerve fibers that appear to be either associated with the corpuscles or are passing though the region.

Pacinian corpuscles, along with thinly myelinated peptidergic nerves. Robert Bowker Files.

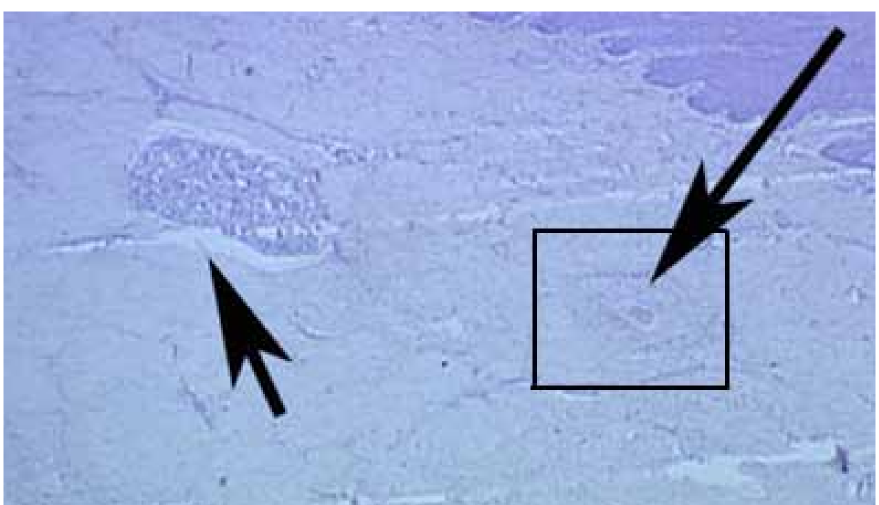


Figure B: A photomicrograph of a section cut perpendicular to the length of the frog showing the epidermis (light blue color in upper right corner) and the dermal and subdermal tissues. The large arrow points out the glands that secrete material onto the epidermal central sulcus of the frog where bacteria aid in creating a "scent" for the horse's communications (similar to the glands opening onto superficial skin of our axilla and groin). The long arrow points to a Pacinian corpuscle near the frog surface that can be activated during stance as well as detect vibrations passing though the ground—from other horses running or even earthquakes. Bar: 400 microns

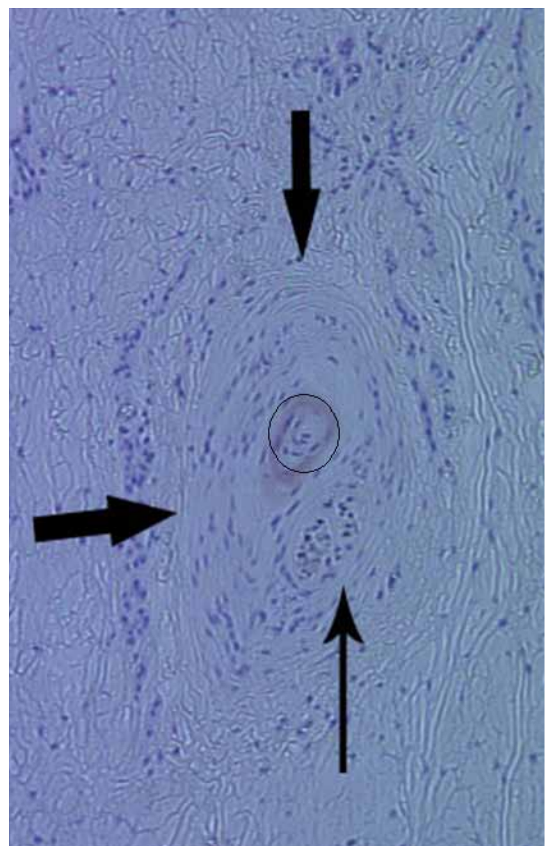


Figure C: A higher power view of the corpuscle with the central axon being outlined and the boundaries of the corpuscle (larger arrows) while a smaller arrow points to another axon passing near the corpuscle. Robert Bowker files.

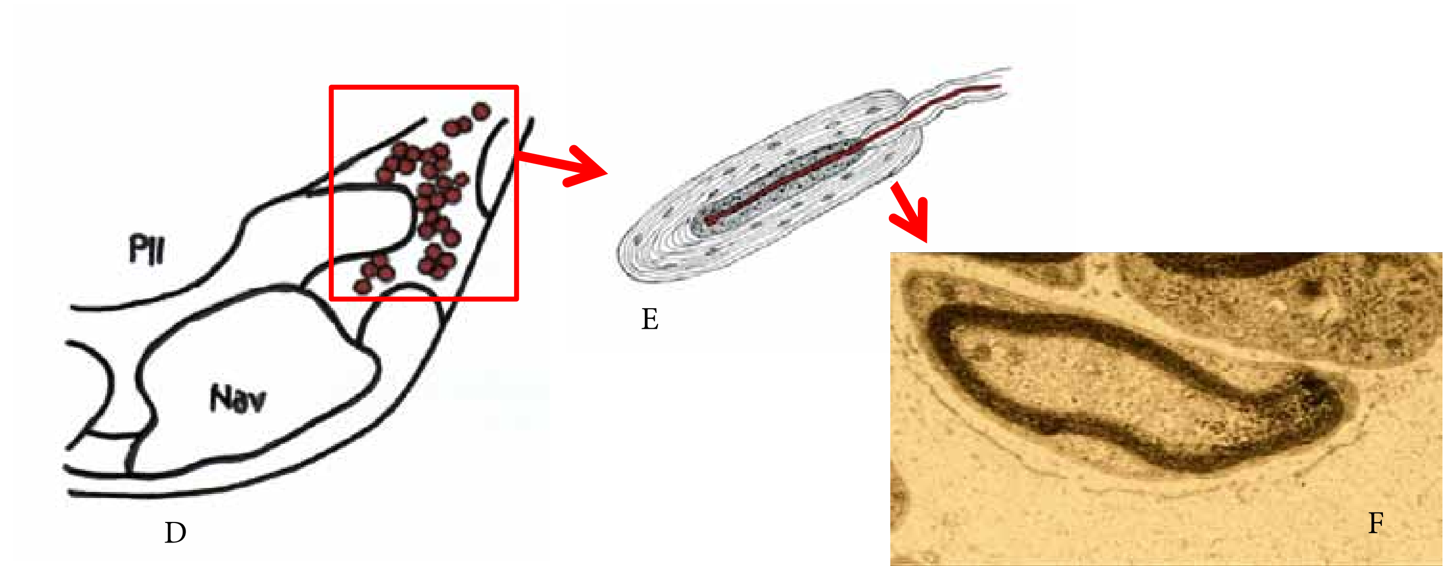


Figure 13D-F: A drawing showing the locations of the tubular Pacinian-like corpuscles associated with the secondary tendon of the DDFT attaching to the distal end of the second phalanx. These mainly tubular Pacinian corpuscles (RED circles) respond in a similar fashion to the more rounded ones—abrupt pressure or stimulation activates a fluid wave within the corpuscle (Figure 13E), thereby inducing an axon potential. The action potential is then rapidly conveyed to the spinal cord via thickly myelinated nerve fibers (Figure 13F) for locomotory reflexes, including the Central Program Generator (CPG) in the spinal cord. In figure 13F, the myelinated fiber is the blacked axon cut in cross section, representing a series of myelin sheaths wrapped around the axon, similar to a "jelly roll". [Nav: navicular bone; PII: middle phalanx]. Robert Bowker files.

Gait abnormalities due to changes in the sensory feedback to the CPG may cause or result in abnormalities or changes in the sensory inputs to these muscles from these receptors present in the feet and distal limbs.[20,23] For example a toe-stabbing gait would result in a mismatch between Pacinian corpuscle input and proprioceptive and touch information from coffin joint and the flexor tendons during the end of the swing phase and beginning of the landing phase, as they probably would not be activated or sufficiently activated to inform the muscles for proper sequence of contraction or the extent of contraction of the muscle fibers. Further, the sensory perception would likely be altered during such foot contact, as Pacinian corpuscles are not evident in the toe area of the foot. If the Pacinian corpuscles are important in the sequencing and coordination of the gait cycle (and neurobiological evidence suggests that they are), then an abnormal footfall of a toe-stabbing gait may disrupt the smooth execution of motor patterns generated in the spinal cord.

The result is stumbling and inefficiency of motion of the affected distal limb that may predispose the horse to further nervous system aberration and potentially other injuries due to abnormal placement of the limb or foot. Similarly, in horses that may have unbalanced front feet, such as "high-low" syndrome or a "club foot", the alteration in the sequencing of the activation of the mechanoreceptors and limb muscles could be contributing to gait abnormalities. The different sensory inputs from the feet will alter the muscle contractions along the entire limb and in the asymmetries of muscular contour at the shoulder, which may be due to disturbances in the central neural pattern of generating muscular contractions. Long-toed and under-run heeled horses may have different sensory effects within the foot during ground contacts.

Similarly, metal-shod horses will quite likely have greater impact energies passing through the foot and to these mechanoreceptors within the caudal foot, which in turn may affect the sensitivity of the neural receptors in the foot during movements.[2,3] Interestingly, in humans, evidence indicates that when the higher frequency energies are greater than 2000 Hz, nerve damage begins to occur in the wrists and lower arms of construction workers, and of secretaries performing repetitive movements, such as typing. These moderate frequency waves damage the thickly myelinated mechanoceptive nerve fibers which, as we have been discussing, convey both touch and proprioception sensory information to the spinal cord to aid in our movement patterns. The more thinly myelinated nerve fibers conducting painful sensations to the spinal cord are less (or are not) affected by the higher frequency energy waveforms. These findings are interesting as we do not know the potential impact of high-frequency energies generated during ground contact upon the sensory fibers of equine foot. This idea may be important to the long term health of our horses.

In addition, recent experimental evidence suggests that Pacinian corpuscles can also respond to low frequency vibratory signals (infrasounds; 20-50 Hz) during stance.[44] The presence of Pacinian corpuscles in the caudal and superficial parts of the frog near its spine (frog stay) suggest that when the frog is in contact with the ground surface, such vibrational energies may be detectable and perceived by the horse. These findings become interesting when one considers that the vibrational energies produced by earthquakes deep in the underground are within the energy response range of Pacinian corpuscles. Such low-frequency vibrations passing through the ground, often days in advance of the actual surface eruption, may be detectible by the Pacinian corpuscles within the horse's foot during stance, which would then be perceived.

Other anecdotal observations suggest that Pacinian corpuscles may be capable of detecting reflected sound waves from large rocks and boulders deep in the ground that are produced during trotting or galloping. During foot impact, the produced infrasound waves would emanate through the underground terrain and then be reflected back to the horses and detected by the Pacinian corpuscles, when potentially treacherous rocks and boulders are about to be encountered ahead—even though the surface features may not be noticeably changed. Many anecdotal observations have mentioned that galloping horses begin to slow down as they approach such underground terrain differences. This vibration detection may explain the many anecdotal and scientific observations that many ungulates can "hear" with their feet!

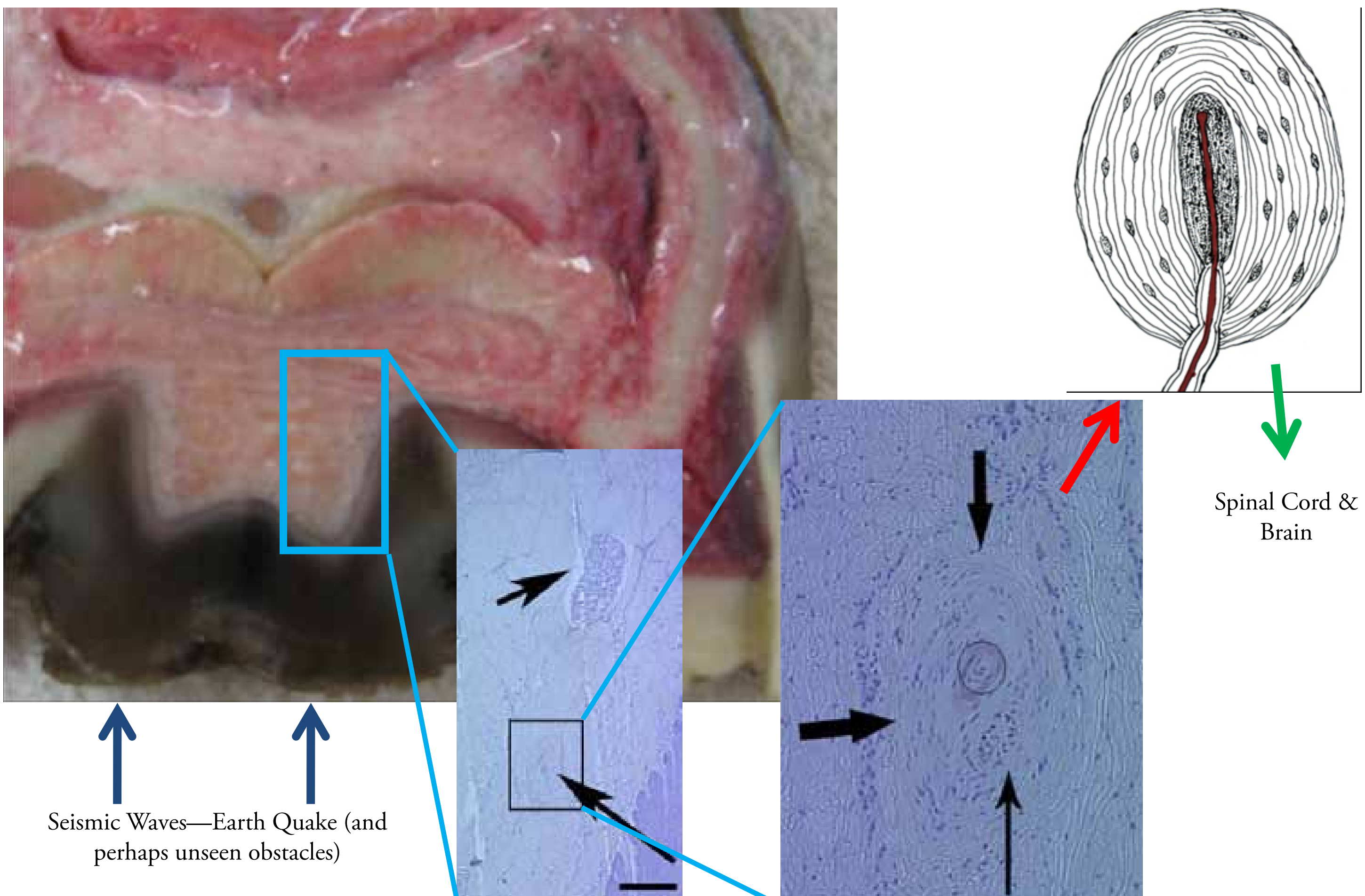


Figure 14: Figure showing a cross section of a horse's foot and the locations of the Pacinian corpuscles in association with the frog. In figure A through the frog, the Pacinian corpuscles are located in the corium but near the surface of the frog epidermis (enclosed area). A histological section through this region shows the presence of glands within the horse's frog that function as scent glands (short arrow) as they open up onto the floor of the central sulcus. The long arrow points to the Pacinian corpuscles, which are typically rounded, as opposed to the more tubular ones associated with the secondary tendon of the DDFT. Figure 14C is a close up of a cut through the corpuscle showing the layers of the fluid filler spaces and the central nerve fiber. The broad arrows demarcate the edges of the corpuscle while the small thin arrow points out a nerve fiber in cross section. Once the nerves fibers are activated by the seismic waves (BLUE arrows) through the ground, such as during an earth quake, this activity is transmitted to the spinal cord and brain for perception. Robert Bowker files.

Furthermore, the palmar locations of the Pacinian corpuscles and the openings of the scent glands onto the zone of the central sulcus of the caudal frog, suggest that foot loading provides a "neuroexocrine" function for the caudal foot. Sensory information is transmitted to the spinal cord for reflex coordination of limb muscles and joints through activation of the Pacinian corpuscles, while the scent glands opening onto the central sulcus permit the apocrine-type secretions to be deposited on the ground during foot contact, enabling communication between horses through olfactory senses.

Ruffini corpuscles and endings:

These sensory receptors appear to respond to light pressure or stretching and have a slower response to changes in the tissues than the Pacinian corpuscles. Ruffini corpuscles have been found in various connective tissues from fibrous to tendons and ligaments[15,16] (Figure 15). These receptors are also present in association with the lateral cartilages as well as in the solar dermis of the foot. In most animals, they appear to respond to continuously applied stimuli, providing sustained information about pressure to the feet of the organism. Their shapes appear to vary slightly depending upon the species as well as the tissue located.[41] Presumably these Ruffini corpuscles present within the dermal tissues will be active along with other stretch receptors during stance when the tissues are compressed or stretched as the horse shifts weight from one limb to another. These receptors are also present within the loose connective tissues of the neurovascular bundle between the foot and the fetlock, which may be activated during limb movements with the stretching of the loose connective tissues of the distal limb.[15]

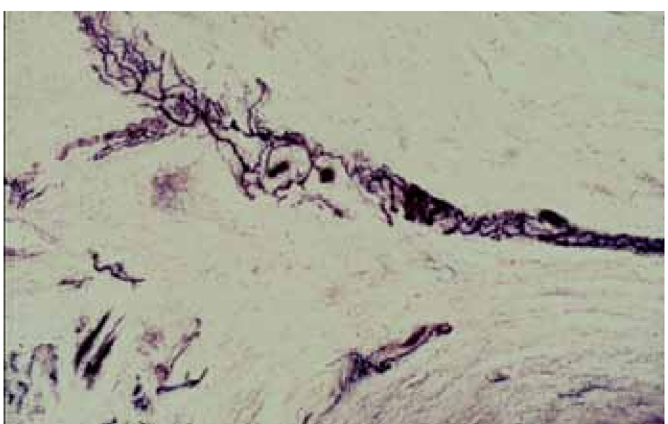


Figure 15: Photomicrograph of a Ruffini-like ending surrounding the neurovascular bundle along the pastern and into the foot. These are similar to other described receptors that respond to the stretching and movements of the loose connective tissues around the distal limb of the horse. Robert Bowker files.

Clinical and Physiological Significance

The clinical significance of these cutaneous receptors (free nerve endings, Merkel discs) and subcutaneous mechanoreceptors (light pressure or stretch receptors and Pacinian corpuscles) of the distal limb, in the palmar/caudal and solar surface of the foot is that they provide the horse with critical information that becomes incorporated into the centrally programmed generator (CPG) in the spinal cord for movement. Many reflex responses are coordinated between the muscles and connective tissues of the limbs during movement. During lameness or gait abnormality, either due to pain or other changes in movement, certain sensory information becomes "deleted" or dormant from the CPG of locomotion and reflex mechanisms in the spinal cord, especially with long-term gait changes. Abnormal afferent input results in abnormal output. In other words, if the sensory messages into the spinal cord and brain are impaired, such as they do not "get into the spinal reflex loop," the motor pattern messages to the limb muscles also become impaired. This can set up a cycle of pain or abnormal locomotion that can be self-perpetuating and lead to further injury of the horse as the gait is now altered and the neuromuscular control may not be properly sequenced. Such movements may lead to improper loading and hence injury of other ligaments, muscles and limb joints of the horse.

For example, with palmar foot pain, some horses move with a characteristic short-strided, "toe-stabbing" foot impact that tends to cause stumbling. Presumably, due to pain in the foot, the horse alters its gait in an attempt to reduce the pain of the foot landing and loading. Removing the source of pain (mechanically by trimming, booting or shoeing and/or medically with analgesic or other drugs) may allow the palmar foot to heal and permit the return of a more normal gait.[3,20,24,35] But in some cases, particularly those with chronic pain, even removing the source of pain does not result in return to a normal locomotor pattern. Research has shown that as feet get long in-between trimming/shoeing appointments, hoof angles change[3] and different hoof angles are associated with different landing patterns,[20] which in turn may affect the integration of the sensory and motor signals in the spinal cord.

When spinal reflexes result in abnormal limb and foot mechanics, it can appear to the observer that the horse has forgotten how to move or stand normally. Owners may comment that their horse is clumsy or doesn't seem to know where its feet are. In these instances, the horse may not necessarily be ataxic like it would be with neurologic disease, or lame like a horse with obvious foot pain. But if the owner sees something amiss with the posture or gait they may ask their veterinarian to examine the horse.

Orthopedic and neurologic diagnostics, including nerve blocks and radiographs, often reveal a horse to be within normal limits despite performance complaints. These may be cases of functional impairment primarily of sensory input, and subsequent motor output changes, that can be amenable to physical medicine techniques in an attempt to reset the proper sequence of CPG reflexes to re-engage these sensory receptors within the foot.

Physical medicine is the application of somatic input to tissues in order to assist return to normal sensory and motor function. Some of the more commonly recognized techniques of physical medicine used by equine veterinarians include acupuncture, chiropractic, massage, and physical therapy exercises. Applying some of these principles to the hoof, there are specific techniques to improve hoof and limb neuromodulation.

Sometimes just rebalancing the hooves will improve movement. If re-balancing the foot is not enough to establish normal locomotion patterns, additional rehabilitation may be needed. The goal is to normalize the CPG neuronal circuits to enable a return to the appropriate locomotor pattern. Equine neuro-rehabilitation is relatively new in veterinary medicine but long-established principles from the human rehabilitation field apply. The goal of rehabilitation is to establish normal joint motion and movement patterns.

When abnormal movement patterns have become habitual, the nervous system adapts and undergoes re-programming of the CPG to accommodate the abnormal postural stance and movement patterns.[23,54] The rehabilitation principle to reintegrate and reinstate normalization of the CPG makes use of these sensory receptors and the reflexes that result when the receptors are physiologically activated. In order to correct established "bad habits" of posture or movement, techniques of rehabilitation use non-habitual movement or touch.

Unfamiliar sensations activate various mechanoreceptors that have been *asleep*. These receptors need to be stimulated so they can once again *talk* to the nervous system in a way that promotes normal stance and movement. Our clinical goal is to normalize stance and movement by providing input to the spinal cord and brain.

Wearing weights or different materials on the feet (i.e. ankle bracelets or wraps) or placed on other body parts changes awareness of where the limbs are located. In the equine world familiar applications of these principles include pastern chains or shoeing alterations to encourage the sought-after high flight arc of gaited horses.

One form of therapy aimed specifically at mechanoreceptors in the feet includes the use of hoof pads placed to preferentially activate receptors in the caudal hoof. This can be accomplished by several methods: In feet shod with pads, temporarily attach an additional pad (2-3 inches long by 1/4-1/2 inch thick or more so that it touches the ground) made of a piece of firm material (such as part of an old hoof pad). In the unshod foot, hoof boots can be used. In some horses just putting on a boot will be enough to correct the movement pattern. Others will need a support pad placed inside the hoof boot. The pad in the boot is placed at the base of the frog so the skin of the heel bulbs is in contact with the material. This placement will activate the sensory mechanoreceptors located in the caudal heel region. As result the horse will usually extend the limb enough to avoid the toe-stabbing movement. This resultant change in locomotor behavior is due to the sensory neural activity influencing the spinal reflex locomotor generator mechanism. Once these original movements are achieved, some horses will be able to move normally without the pad right away. Others will need periods of rehabilitation, wearing the pads for a few days or weeks before the proper gait reflexes are reestablished.

Physical therapy can accomplish this by activating mechanoreceptors not only in the feet, but all over the body. Beyond hoof specific manipulations, additional sensory input can be used to elicit particular motor patterns with the goal of improving gait. Walking on different ground surfaces activates receptors from the soles that transmit messages to the spinal cord and brain that coordinate balance and movement. The use of elastic body wraps (Thera-Bands) or elastic skin tape (Kinesiotape) provides sensory input that improves kinesthetic awareness. This is a form of neuromotor training that improves sensory integration. The result is what owners wish to see in their horses: more coordinated, graceful and efficient movement as the horse engages in activities under saddle or freely moving in their pastures.

During every foot-to-ground contact, the mechanoreceptors are activated, which initiates the central propagation of the sensory information to the spinal cord and brain, as we have mentioned above. However, the sensory nerves also engage and activate other physiological events within the foot simultaneously. These other triggered local events enhance the detection and perception of various ground stimuli and reduce the biomechanical stresses within the foot, as well as alter the perfusion of the horse's foot.

When standing on hard surfaces, such as cement, the solar surface area of ground contact on the horse's foot is reduced. This firm surface results in a greater biomechanical stress (weight load/ unit area) than when on conformable surfaces.[15]

Minimal solar contact is evident, as a thin probe can be passed freely under the foot, except the wall areas (pastured barefoot horses) contacting the cement, while on a more conformable surface, greater contact areas are evident (Figure 16). Presumably the activation of different sensory receptors within the foot occurs as differences in the physiological effects on blood flow through the foot can be detected and measured, using Doppler sonography. In addition, the effects of activation of sensory nerves can be seen in changes of blood flow in the opposite foot (see below).

Measuring Blood Flow with Doppler Ultrasound

Briefly, Doppler ultrasound uses reflected sound waves to evaluate fluid movement relative to a recording device; in this instance the characteristics of the red blood cell flow.[18] The difference between the frequency of the transmitted ultrasound waves and the reflected wave frequency is directly proportional to the velocity of the reflecting interface relative to the receiver. This difference, or Doppler shift, is measured in centimeters per second (cm/s). The computer uses the frequency information and a mathematical equation to calculate and display the velocity of blood. When recording a Doppler sonogram the information gathered is displayed as a Doppler spectrum (Latin for "image"). This electronic display of velocities of blood flow through a specific vessel sampled is plotted as a function of time that can be quantified. The key elements in the image are velocity (Vertical Y axis) and time (Horizontal X axis), while other secondary information (called indices) can be gathered to describe the fluid flow through the vessels when the waveforms are examined closely. The anatomy of an arterial waveform is displayed on the spectral diagram below. Flow direction is shown in relation to the spectrum baseline. Flow towards the transducer is shown above the baseline, whereas flow away from the transducer is shown below the baseline.

A variety of mathematical formulae can be used to describe the arterial pulsatility, and include the Systolic/Diastolic ratio, Resistance Index, and Pulsatility Index. These measurements and calculations are generated by the ultrasound computer and aid in the descriptions of arterial resistance of a given vessel to ascertain the physiological and/or pathological status of the vasculature and its flow.

The characteristics of blood flow are influenced by the energy (driving force or pressure) generated by the cardiac cycle and the physical features of both the vessels and the blood cells. The vasculature contributes to the resistance opposing forward movement of fluid through the vessels via friction and constriction. In Doppler recordings from the vessels of the horse's distal limb, the foot, enclosed by a keratinized shell, serves as a unique and additional modulator of the blood flow to and from as well as through the foot, as it is "centrally located" between blood flow of the palmar digital artery (PDA) entering the foot and the venous blood flow of the palmar digital vein (PDV) exiting the foot. Such a centralized location means that any changes in flow characteristics of blood entering and exiting the foot and passing through the foot, must be due to alterations in the physical effects and the neurophysiological activities upon the vasculature. These changes will be reflected in the different parameters recorded using Doppler ultrasound.

Figure 17a, b, c The schematic waveforms on pulsatility.

(Low) (Moderate) (High)

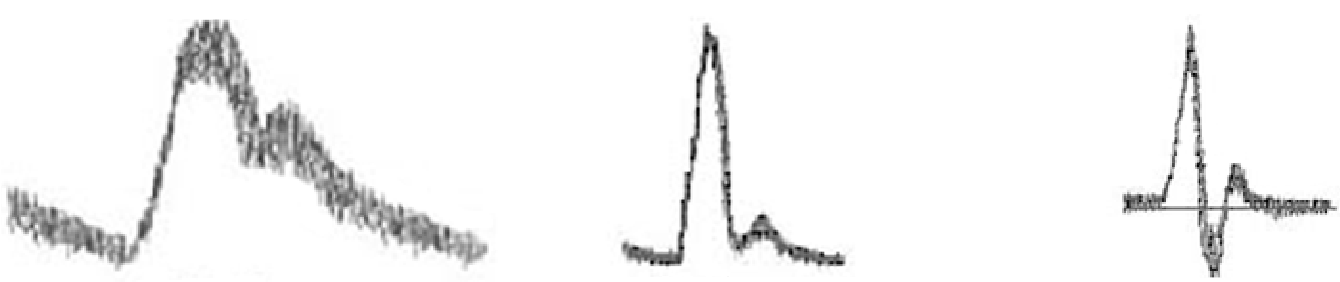
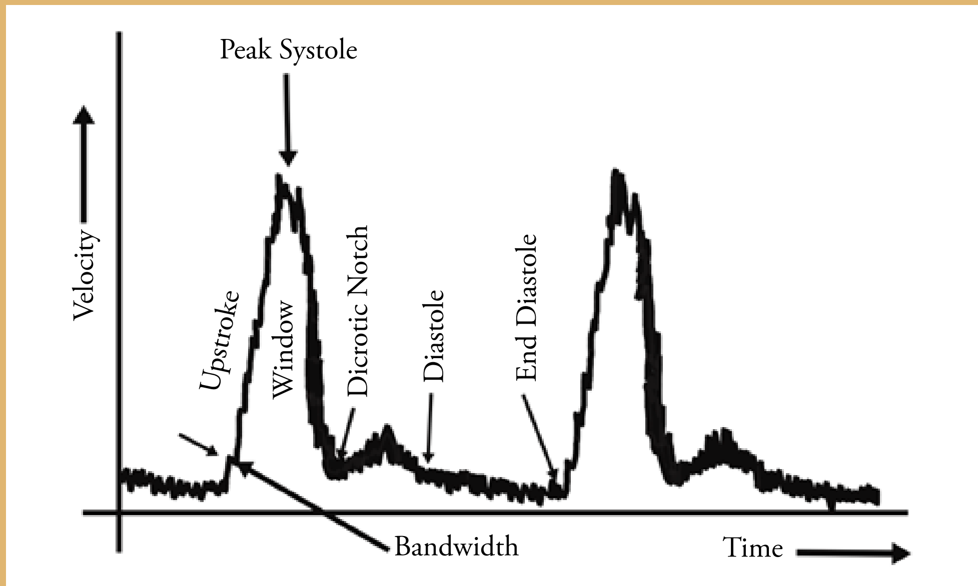


Figure 17: Doppler waveforms showing the variation in pulsatility or how rapid the pulse wave is achieved. Low pulsatility means that the wave pulse reaches its peak slightly slower (greater time period) than other waveforms with a high pulsatility wave being very rapid. In the high pulsatility wave, the peak is achieved quickly, as most of the blood flow detected by the probe has similar features. This rapid rise to peak pulse would be often observed in a horse with laminitis and often described as a bounding digital pulse. Robert Bowker files.



Descriptive Terms of Waveform Anatomy:

1. **Peak Systole or Peak systolic velocity:** Point of peak velocity of flow in cardiac cycle.
2. **Dicrotic Notch:** The dicrotic notch literally means "the second part of arterial pulse" and indicates aortic valve closure. It separates the systolic from the diastolic part of the arterial pressure wave.
3. **End Diastole:** Point at which the blood flow reaches its low velocity just prior to the next systolic upstroke.
4. **Window:** The "clear area" under the systolic peak that displays no frequencies.
5. **Bandwidth:** The range of velocities sampled within the vessel. More turbulent flow will indicate a greater range of velocities.
6. **Waveforms and Pulsatility:** In arteries, each cycle of cardiac activity produces a distinct "wave" on the Doppler velocity spectrum. The term waveform refers to the shape of each of these waves. **Waveforms** are described in terms of **pulsatility**, reflecting the type of characteristic arterial resistance supplying various parts of the body. **Low-pulsatility** waveforms reach peak velocities more slowly and thus have broad systolic peaks and forward flow throughout diastole as there is less resistance downstream. These vessels feed circulatory systems with low resistance to flow such as when many of the vessels located downstream are open most of the time. In humans the vessels to the kidneys and brain are observed to have this waveform. Low pulsatility waveforms are also referred to "Monophasic" meaning flow is always forward as the waveform is above baseline. **High pulsatility** waveforms reach peak velocity rapidly and show a tall, narrow, sharp systolic peak and a reversed or absent diastolic flow due to a greater peripheral resistance in the arterial vessels downstream. The classic example of a high pulsatility waveform is the **triphasic** flow pattern seen in peripheral arteries. A sharp forward flow, systolic peak (first phase) is followed by brief flow reversal (below baseline; second phase) and then by brief forward flow (above baseline; third phase). Often during the diastole the blood flow as seen in these waveforms is absent or reversed due to the high resistance to forward flow. Between the low and high pulsatility waveforms are the so-called **moderate pulsatility** waveforms, which have an appearance somewhere between the low and high resistance patterns. With moderate pulsatility flow resistance, the systolic peak is tall and sharp, but forward flow is present throughout diastole, as opposed to the high pulsatility waveforms. Physiology and pathology may alter arterial pulsatility. Examples of low, moderate, and high pulsatility waveforms are shown at left:

The foot is usually loaded during Doppler ultrasound recordings of the horse, which is in contrast to human recordings, where the patient is usually lying horizontally with no loading of the limbs. This fact means that internal and external physical influences acting upon the foot in the standing horse (i.e. non-weight bearing, weight bearing, surface, shod versus non-shod, extravascular (interstitial) pressures, etc.), will not affect, or at the very least, be less influential in altering fluid flow through the different vascular beds in man. However, in humans, vascular disease is more prevalent than in the horse, which is a primary reason for Doppler ultrasound's usefulness in human medicine. The neuroreceptors present on the vasculature (see above) will serve as "gate keepers" of the fluid flow as they can control the regional perfusion through the foot, by permitting or restricting flow through various vascular beds within the foot prior to its exit via the digital veins. As a result, these receptor and neurological "gate keeper" effects will influence the recorded parameters of the Doppler waveforms as blood passes through them at different times. ***By recording from the PDA and the PDV along with utilizing the above mathematical descriptive terms for flow during the cardiac cycle, one can obtain a reasonable approximation of the status of the physiological perfusion of the horse's foot under the conditions of the recordings.***

The venous vasculature of the thoracic and neck of humans and of the horse are under the influence of the cardiac cycle and of alterations in the intrathoracic or abdominal pressure. These pressure changes within the thoracic cavity will produce an increased flow and venous volume during inspiration, while the opposite occurs during expiration. So the Doppler venous wave form undulates in synchrony with the respiration. Changes in abdominal pressure can affect blood flow and volumes through the venous microvessels and larger veins in the lower limbs in both humans and horses (Valsalva maneuver, during defecation) as well. Otherwise, the veins in humans do not pulsate. In contrast, the veins of the horse's distal limb do pulsate, apparently with their own intrinsic rhythm (unpublished observations). The veins in other regional body areas do not pulsate. In figure 18 of the PDV recording obtained at the level of the lateral cartilages, one can see the pulsating waveform of the vein.

The physical characteristics of these arterial and venous waveforms provide quantitative and qualitative information about the blood flow through the specific vessels sampled. And because the recording site is at the lateral cartilages or the fetlock joint, the waveforms also tell us about the physiological state of the vasculature within the foot, in accordance with fluid biophysical theory. For example, the arterial pulse waveforms at these sites will be influenced by the many different microvascular beds situated downstream

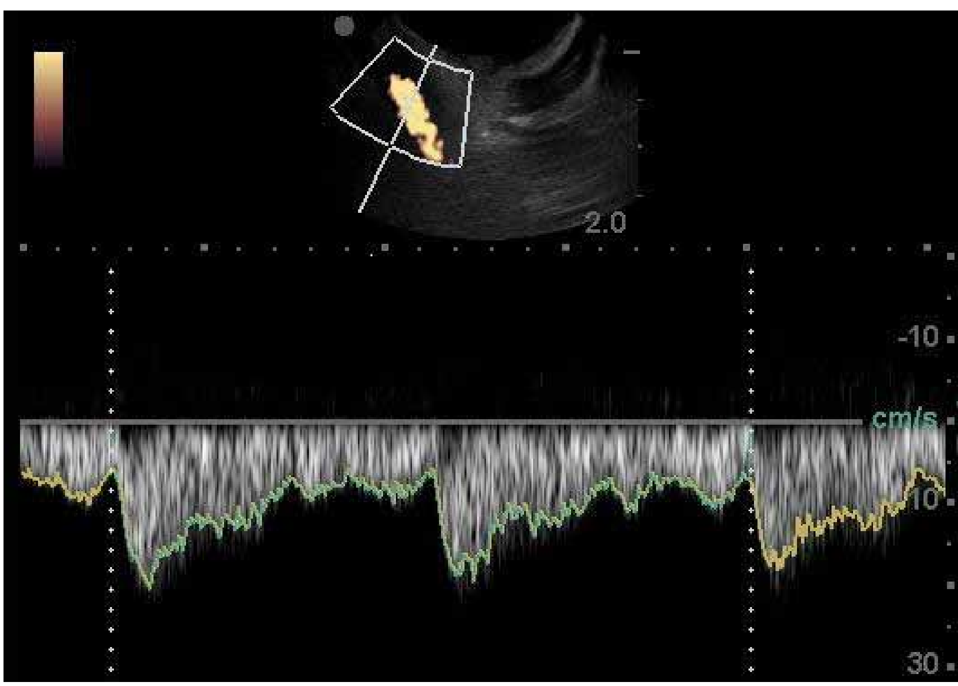


Figure 18: Doppler recording of a pulsating vein observed at the level of the fetlock showing the downward excursion of the pulse. The horizontal axis indicates time while the vertical axis is speed of flow (cm/sec). The downward pulse is systolic wave due primarily to the generated waveform by the smooth muscle in the PDV. The waveform between the venous contractions is referred to as diastole when flow is determined by Poiseuille's law, or the physical features of the blood fluid and the vessel. The faster that the waveform returns to baseline the greater resistance there is within the vascular bed, and vice versa.
Robert Bowker files.

within the foot. This influence will depend upon the extent that the arterial/venous circulation within the foot that is opened and/or closed. With all the microvessels open, many of the small vascular channels and regional vascular beds are now accessible for the blood flow to enter them within the foot. Such vascular openings will result in reduced blood flow velocities, pressures and other waveform characteristics (low pulsatility) across the vascular beds. As more and more vessel openings occur and the relative lengths of the vascular networks increase (i.e. fluid flow biophysics), such actions are similar to adding drip hoses onto your main hose for watering your lawn.

With all or most of the microvessels open, the total blood flow through the foot will generally remain relatively unchanged. The arterial waveforms recorded during these times would be examples of low pulsatility waves. At the other extreme when all microvascular beds are closed or have restricted flow through them and the foot is loaded, most blood flow in the foot would be confined to the largest vessels within the foot. These changes result in higher velocities of arterial flow, more sharply defined systolic waves and a rapidly decrescendo in fluid flow during diastole as the resistance within the foot becomes higher (e.g. fewer open vascular channels). During these times, the arterial waveforms may even become triphasic waves, which have the highest pulsatility.

On the venous side of the equation, the same microvascular beds within the foot can influence the blood flow entering the PDV, and hence the venous waveform characteristics. Flow velocities and vascular pressure will also differ depending upon the internal or external forces impinging upon the foot tissues. After the arterial blood flow enters the foot and traverses through opened arterial and venous microvasculatures, the ultrasound waveform characteristics of the exiting venous flow are reduced from the arterial waveforms, including velocities, acceleration and the driving pressure differences in accordance with fluid hemodynamics. The opposite generally occurs when the microvascular beds are closed, as the velocity of fluid flow through the remaining open vascular beds is higher. The recorded waveforms under these different recording situations will also demonstrate indices of relative higher pulsatility, velocities and acceleration, but will be less dramatic than those waveforms recorded from the arteries.

An understanding of these waveform characteristics as they relate to the blood flow through the horse's foot and fluid hemodynamic theory will provide the veterinarian with critical information regarding the physiological status of the horse's foot. In the horse, only a few reports have assessed blood flow through the foot, using Doppler measurements.[21,34]

Influences on Blood Flow Through the Foot

With this very basic introduction to Doppler ultrasound, we wish to illustrate that the sensory activation of mechanoreceptors can influence and change the blood flow and its tissue perfusion within the horse's foot. In the first example differences in perfusion of the horse's foot can be observed when the horse stands on different ground surfaces. In figure 19A the horse is standing on a cement block, while in figure 19B the same horse is standing on a conformable surface (pea rock bed), mintues later. As we assume a similar volume of flow to the foot (consistent with other flow measurements), the velocity of the blood flow remains higher on cement [greater peak systolic (PSV) and End Diastolic velocities (EDV)] in comparison to when the horse stood in a bed of pea rock a few minutes later [PSV- 41.4 cm/sec versus 35.0 cm/sec, and EDV-8.37 cm/sec versus 6.17 cm/sec, respectively].

These differences in perfusion through the foot vasculature suggest that on the conformable surface, more opened microvessels permit greater flow through them as evidenced by a reduction in PSV and the EDV, i.e. more vessels are open for fluid *run-off* (Figure 19C). Other changes in waveform characteristics of both the arterial and venous recordings are consistently observed, supporting this interpretation. These observations suggest that different ground surfaces may be activating (or not activating) different sensory mechanoreceptors on the solar surface of the foot, which in turn may affect the perfusion of the horse's foot (Figure 19D). When the horse is standing on a layer of Terri cloth towel, we assume that the tactile and/or the light pressure receptors are being activated (Note: experimentally it is difficult to distinguish between tactile and light pressure stimulation of receptors).

The next observation provides more positive evidence of the significance of the mechanoreceptors and the neurological effects affecting the vasculature and blood flow of living tissues. The activation of these touch and light pressure sensory nerves can often over-ride the effects of increased loading and internal compression of the vasculature within the foot (i.e. more than 500 pounds on one foot). A more dramatic observation occurs in the venous vasculature with a horse standing on cement, and elevating the opposite leg (Figure 20A). This loaded leg position nearly doubles the load on the weight bearing foot from which the recording is taken. When double-loaded a greater internal resistance to blood flow through the foot occurs: blood flow is moving slowly forward (downward-low velocity), backward (upward), and at times not moving significantly (baseline flat).

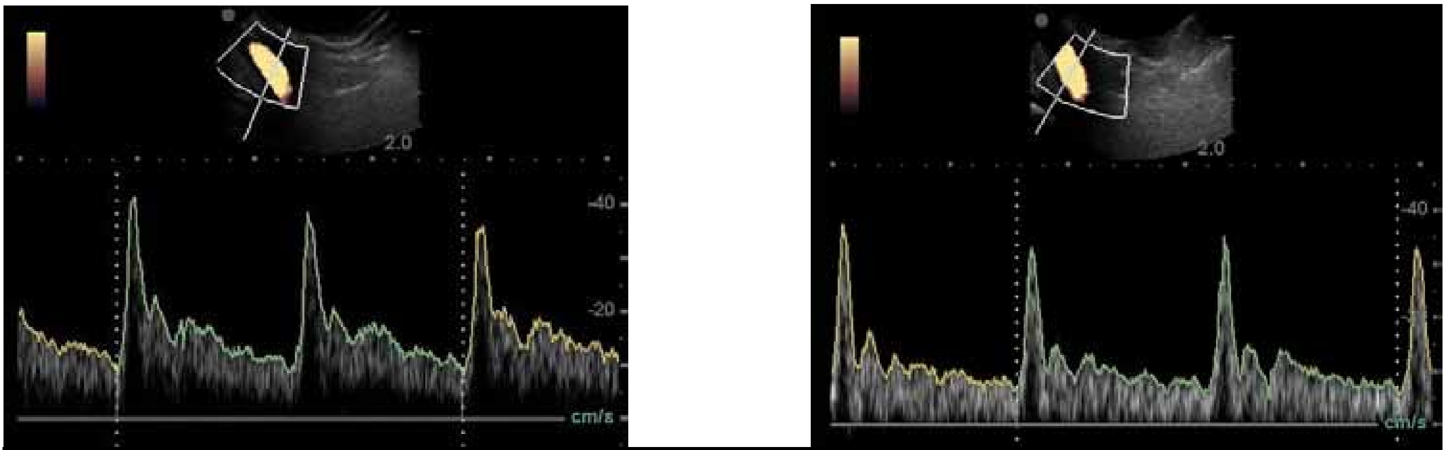
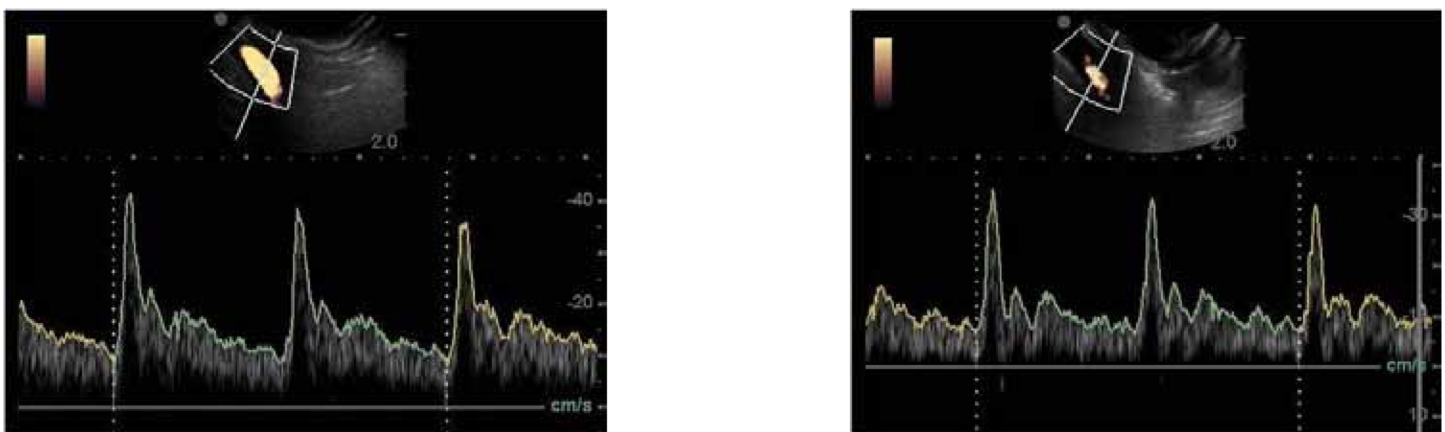
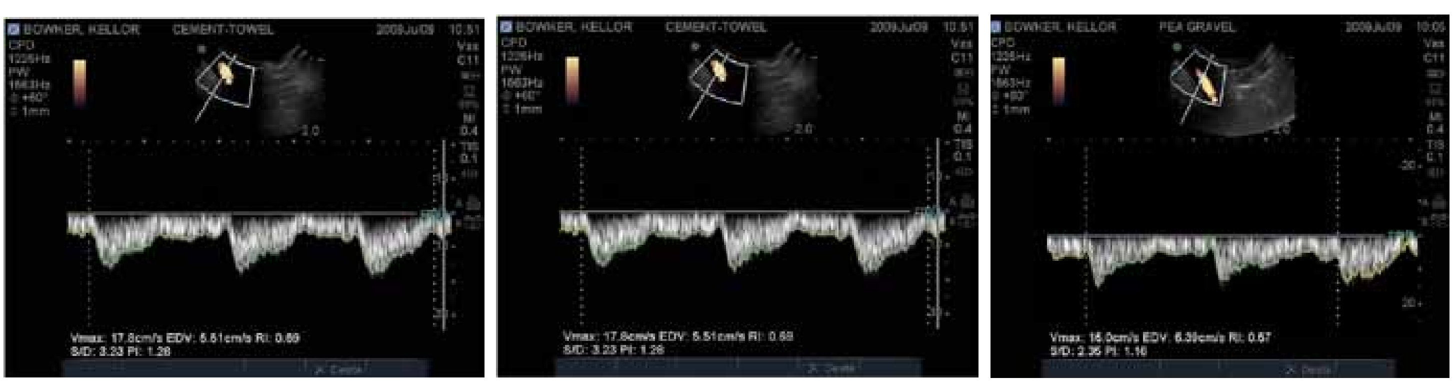


Figure 19A, 19B: graphs of Doppler ultrasound showing that the tissue perfusion and flow through the foot does appear to change depending upon the ground surface that the horse is standing on. In Figure A (left) the horse is standing on a cement block and shows that the flow velocity is higher (see text) than when the same horse is standing on the conformable surface of pea rock minutes later (Figure B right). Robert Bowker files.



In figure 19C (left), direct comparisons of the two graphs shows that the slopes of the flows is greater when standing on the cement as compared to the conformable surfaces. In Figure 19D a difference is apparent between cement alone and cement with a layer of Terri cloth towel. Robert Bowker files.



In Figures 19E-G the PDV is recorded showing changes in the venous flow from the foot when on cement (E left), cement but standing on a Terri cloth (F center) and finally on a bed of pea rock (G right). Briefly when standing on the conformable surface, the end diastolic velocity (EDV) and vessels resistance index is lowest of the three when compared to the recordings on cement. These observations are consistent when the vascular beds have a greater openings. Robert Bowker files.

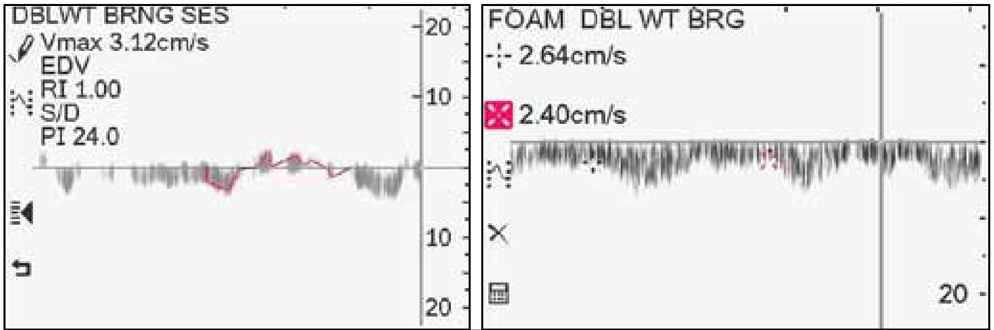
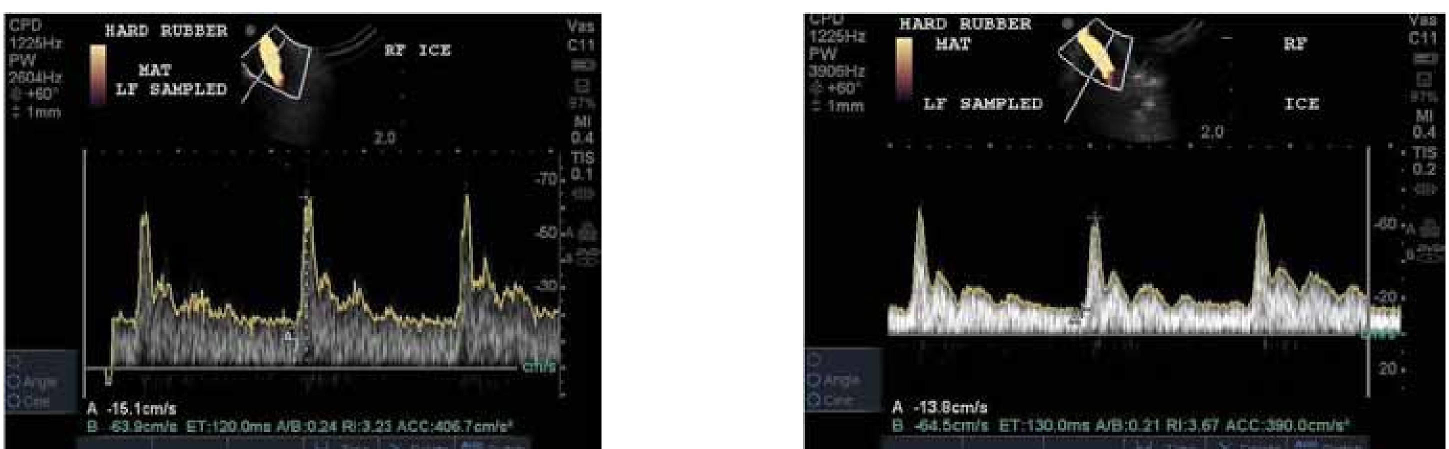


Figure 20A (left) is a graph showing flow through the PDV when the horse is standing on a hard surface and one leg is elevated. The flow through PDV of the foot is compromised due to the double loading of the foot (recording from the loaded foot while the opposite one is elevated). Blood flow can be seen to go forward slightly (below line in graph or backwards: upward deflection) or not be flowing at all at the level of the fetlock. However in Figure 20B (right), the flow through the PDV at the level of the fetlock improves when the same horse stands on a thin foam pad. The flow is always forward (below line) and one can see the pulsations in the PDV. Robert Bowker files.

In some horses, blood flow actually stops for periods during diastole (between heart beats). In figure 20B, performed less than a minute later on the same horse, while the horse stood on a conformable surface (thin foam pad or Terri washcloth) placed on the same cement block, the venous blood flow improves (as indicated by the increased forward flow) and the return of normal venous pulsations. These two observations suggest that the activation of mechanoreceptors on the solar foot will promote vasodilatation of the vasculature beds, similar to the effects observed in humans.[28] The sensory stimulus provided by the Terri cloth or pad may have affected the arterial and venous blood flow through vascular beds within the foot, potentially operating via SP, or similar neuropeptide receptors present on the microvasculature.[56] The mechanoreceptor stimulation from the conformable surface may increase the perfusion through the entire arterial, micro- and venous vasculature or through one portion of it, even during the doubly-loaded condition. Future works will have to sort this interesting question out.

On another note, a common belief is that fluid and blood flow through the loaded foot ceases due to the increased pressure within the foot. Several experiments have been employed during experiments, when a limb obtained from a cadaveric (i.e. dead) specimen is loaded, and fluid is infused through the vasculature to simulate blood. In these experiments when the foot is compressed, the "blood" is squeezed from the foot, which in turn prevents, or at the very least reduces, fluid flow through the foot. This experiment is similar to the "doubly loaded" foot in the adult horse when standing upon a hard non-conformable surface, as mentioned above. Under these conditions within the cadaveric foot, the effects and influences of live sensory nerves upon the vasculature and fluid flow are eliminated, as these tissues are basically dead and not responsive. However, in the live horse, the sensory nerves can be activated via the tactile/light pressure receptors and can affect vascular perfusion through the foot. This simplistic idea that the cadaveric models are similar to the live horse has a few obvious problems.



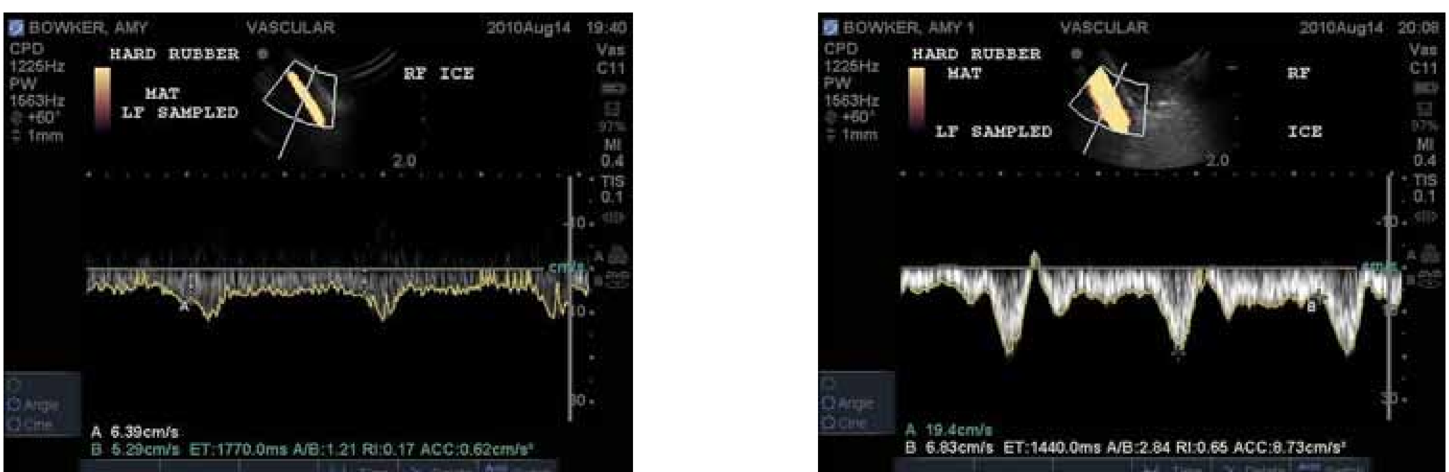
Figures 21A and 21B: In these figures, blood flow through the PDA of the foot before the opposite foot was place in a shallow pan of ice and water (Figure 21A), followed by changes in the non-iced limb a few minutes later showing that the blood flow was reduced due to a vasoconstriction mediated by the sensory nerves. The reduction in almost all parameters in the non-iced foot (normal ambient temperature) is consistent with a generalized vasoconstriction being mediated by the sensory information from the opposite iced foot affecting the blood flow in the opposite non-iced and normal foot. Robert Bowker files.

Interestingly, the sensory nerve activation can also have effects at distances beyond where the stimulation was being applied. We have observed the effects of sensory nerve stimulation with a cold thermal stimulus applied to one foot immersed in ice water to the level of the coronet and recorded the vascular effects of opposite non-iced foot. In Figures 21A and 21B, the blood the flow through the normal foot was examined in both the artery and vein, respectively, recorded at the pastern and fetlock levels using Doppler flow ultrasound technology while a horse was in a stance posture. Within a few minutes (~5 minutes) the vascular blood flow patterns began to change in the non-iced condition as the velocity of flow, pulsatility and other vascular parameters changed as the vascular resistance increased.

These vascular changes in flow parameters are consistent with a reduced fluid flow through the foot due to constriction of blood flow through the foot. In the iced foot, similar but more dramatic changes in flow parameters, as vasconstriction, were also observed. These changes in the ice condition were due to (1) the more direct temperature effects of the ice condition on the foot tissues and (2) the possible indirect effects of neural vasoconstriction on that side as well. However, in the non-iced condition, the effects had to be neurally induced or mediated as the non-iced condition was in an ambient temperate climate (July in Michigan and California). This example merely illustrates the effects activating the sensory nerves via thermal stimulation (i.e. cold) and perhaps tactile (i.e. foot immersed in water to level near the coronet). While further research needs to be performed as more and more questions need to be answered, at the very least these observations are interesting as they provide potential ideas and mechanisms as to the influences of acupuncture and similar modalities upon vascular flow and perfusion that can be measured physiologically.

Potential Clinical Relevance

Understanding and appreciating the many sensory nerves and receptors present within the horse's foot is important to the clinician during a lameness examination. To the horse, the appropriate functioning of these nerves and receptors are critical to enable the horse to safely negotiate the terrain, however smooth or rough, at all gaits. And these nerve components are important to the rider as their healthy functioning helps to prevent tripping and falls. Activation of sensory receptors may prove beneficial to: (1) the horse for promoting its overall health via improving the status of the neuromuscular reflexes and responses of the back and neck regions, (2) the veterinarian during a clinical lameness examination to enable more specific identification of painful and/or damaged areas within a foot by activating different sensory receptors, and (3) the use of the receptors and their reflexes during rehabilitation



In Figures 21C and 21D, a similar interpretation is observed when recording from the PDV of a generalized vasoconstriction in the opposite non-iced and normal foot. Robert Bowker files.

Summary:

We have provided a brief overview of the neural innervations of the equine foot, documenting that there are many different types of nerve fibers and receptors within the foot tissues. Veterinary medicine has traditionally focused more on pain in dealing with sensory nerves in the distal equine limb and as a result, pain medication has been one of the mainstays of treatment. Other sensory fibers and receptors are present that provide important and useful information to the horse during both stance and movement. These different types of mechanoreceptors are stimulated and respond to the sensations of light touch, pressure varying from light to deep, vibration, and thermal changes to name but a few. These mechanoreceptors are distributed in different regions of the foot.

We believe that the Pacinian corpuscles are appropriately activated when a horse lands normally with a flat or heel-first impact, and are probably also activated by low frequency vibrations arising from deep underground. As tactile and light pressure sensations are known to be important in the activation of normal gait reflexes and posture, there are various ways to utilize these sensory inputs as therapies to reestablish normal gait patterns. We have found clinical success in some palmar hoof lameness cases by using sensory stimulation of the caudal frog with hoof pads that only contact that area and not the whole frog. We propose that attention to sensory systems and neural circuits in locomotion may offer new diagnostic and therapeutic opportunities. This functional neurology focus may become particularly useful in horses with refractory gait abnormalities that cannot be blocked out. And also in those horses that do not respond or incompletely respond to medication and/or trimming and shoeing changes.

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