Genetic Selection for Gaits in the Horse[1]

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What is the connection between locomotion patterns and genetics?

Quality and cadence of various locomotion patterns are extremely valuable traits in horses. Breeds like the Tennessee Walking Horse, Florida Cracker Horse, Mangalarga Marchador, and Icelandic Pony are prized and selected for unique intermediate-speed locomotion patterns. What if genetics could help us unravel and better select for the locomotion patterns of our horses?

All healthy horses are able to perform the basic patterns of low-speed (the walk) and high-speed locomotion (the gallop). However, the patterns can vary immensely at intermediate speed, ranging from the diagonal pattern in the trot to the lateral pattern of the pace. Gaited breeds are prized for diverse intermediate locomotion patterns in which the legs do not pair completely. When listening to these horses move, we are able to discern four distinct hoof beats corresponding to the "four-beat" pattern. This lack of synchronization is the main characteristic of a smooth-gaited horse. Still, in some four-beat gaits there are moments of diagonal pairing and lateral pairing that might resemble the synchronization found in the trot and pace (Figure 1), respectively. One of the most well-recognized and striking moments of limb support in the four-beat gaits is the triple support, when three feet are in contact with the ground at the same time. Much of the comfort felt by the rider in the saddle is indeed attributed to this characteristic (Figure 2).

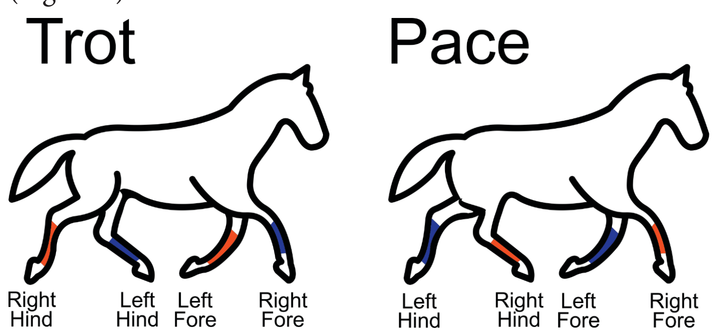

Figure 1. Observe the difference between the airborne (suspension) moment in the trot and the pace. The horse's limbs are colored according to the limb pairing.
Credits: Laura Patterson Rosa, UF/IFAS

In contrast to the pace, an exclusively lateral-paired locomotion pattern, the traditional trot is a diagonally paired locomotion. Neither is considered a true four-beat ambling gait because each possesses a moment of suspension (where the horse has no foot contact with the ground or is airborne) between the change of supporting pairs (Figure 2).

In vertebrates like the horse, locomotion patterns are controlled by the *central pattern generators* (CPGs), a group of neurons present in the spinal cord. Although the exact neurons forming the CPGs are not yet known, scientists have discovered that the CPGs are regulated by genetic factors that "pre-program" the behavior of these neurons.

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The innate, hereditary four-beat ambling gaits may vary between gaited breeds such as the Tennessee Walking Horse, Florida Cracker Horse, Mangalarga Marchador, and Icelandic Pony, but they are nonetheless determined by the CPGs. The CPGs orchestrate motion in a slightly different way in all these patterns of locomotion, "signaling" the legs to move with varied timing and pattern. What is the "code" embedded in the DNA that controls the actions of these CPGs?

Figure 2. (a) Paso Fino, (b) Spotted Saddle Horse, (c) Mangalarga Marchador, and (d) Tennessee Walking Horse showing the moment of "triple support" when three feet are in contact with the ground, which is one of the characteristics of the four-beat gaits.
Credits: (a) Just chaos/Flickr/CC-BY-2.0 (b) Just chaos/Flickr/CC-BY-2.0 (c) Alexandre Augusto, Haras Guariroba—Bahia, Brazil (d) Dan Dee Shots/Wikimedia Commons/CC-BY-2.0

DMRT3 and Locomotion in the Horse

Geneticists recently reported that the change, or mutation, of just a single "letter" within the entire genetic code is able to influence locomotion patterns in a variety of species. The most famous recent example in the horse is a mutation in a gene named *DMRT3* (*doublesex and mab-3 related transcription factor*, *isoform 3*) (Andersson et al. 2012). This mutation turned out to be fairly common within the group of Icelandic horses studied, which included those with the ability to perform five gaits (walk, tölt, trot, gallop, and pace) and those that could only perform four gaits (walk, tölt, trot, and gallop). The *DMRT3* variant is generally found in higher frequencies among some other breeds including the Mangalarga Marchador and the Puerto Rican Paso Fino. It is the most prevalent variety in the Tennessee Walking Horse and the Standardbred (Jäderkvist et al. 2015; Promerová et al. 2014).

A study conducted in the Mangalarga Marchador suggested that, although possibly linked to the type of gait (batida or picada, the two types of gait performed by this breed), the *DMRT3* allele was not the main cause underlying the natural talent for the ambling gaits found within the breed (Patterson, Staiger, and Brooks 2015). Picada horses more frequently possess two copies of the variant allele (a given part of a gene), A/A, while batida are usually C/C. However, this genotype alone is not a perfect indicator of gait type as both picada and batida possess moments of lateral and diagonal movement. It was also found that C/A horses (heterozygous, with one copy of each type of this gene) fall into both categories of gait type. Other studies have reported skilled picada horses with the C/C genotypes. The picada gait is also commonly associated with a more difficult transition to canter and a lower canter quality by breed judges and trainers (Patterson, Staiger, and Brooks 2015).

Is *DMRT3* related to the gait or canter ability?

Although Andersson et al. (2012) suggested that the *DMRT3* variant could be permissive to the ability to perform four-beat ambling gaits at intermediate speed, they also observed that horses homozygous A/A (two copies) for the variant earned lower quality scores for the gallop. In Standardbreds, the presence of the C allele was linked to a more balanced canter and better transition scores in collected canter (Jäderkvist et al. 2015). In Finnhorses, the genotype A/A was linked to an increased ability in trotting harness racing, an event in which horses are disqualified for breaking into the canter at higher speeds (Fegraeus et al. 2015).

Breeds that are not known for ambling gaits can also possess the A variant at a low frequency. One study found heterozygous C/A horses among both Arabian and American Quarter Horse populations, but since their occurrence within the population analyzed was low-frequency, no conclusions could be made regarding these horses' gait characteristics (Regatieri et al. 2016). The variant does not distinguish the lateral and diagonal footfall patterns because both trotting and pacing horses frequently possess the A variant. This is a phenomenon observed in studies focused on the Icelandic Horse (Andersson et al. 2012), American Saddlebred (Regatieri et al. 2017), Standardbred (Jäderkvist et al. 2015), and Finnhorse (Fegraeus et al. 2015).

Higher frequencies of the variant form are found among horses bred for harness racing (Andersson et al. 2012), supporting the theory that the variant form influences the ability to transition from an intermediate-speed gait to the canter. A harness horse with the tendency to move quickly but avoid the canter or gallop is at a considerable advantage on the harness racing track.

"Knocking Out" a Mouse to Improve Understanding of the Gene Function

To better understand the functions of a mutation on this gene, researchers also developed a genetically modified mouse in which the *DMRT3* gene was completely erased. This "knock-out" mouse, lacking the gene and thus the protein encoded by that gene, provided information about the function of the *DMRT3* gene as well as the things that occur within its variant form. This modified mouse could not sustain higher locomotion speeds on a treadmill (Andersson et al. 2012). This difficulty in performing the transition from an intermediate-speed pattern to one of a higher speed is a characteristic shared with horses that have the variant A form of the gene.

For a video of the KO mouse (Andersson et al. 2012), please visit http://www.nature.com/nature/journal/v488/n7413/extref/nature11399-s5.mov.

Lower quality canter and difficulty with transitioning to the canter are frequently found among Mangalarga Marchador horses that are naturally picada gaited. The gait type is mainly correlated to the homozygous A/A form of the gene (Patterson, Staiger, and Brooks 2015; Manso Filho et al. 2015; Fonseca et al. 2017).

Current and Future Applications

As researchers develop better tools to evaluate locomotion parameters, we can improve the classification of locomotion phenotypes to evaluate genotypic variation in more detail. Recent examples of these tools are the Lameness Locator™ (Figure 3), the Automated Gait Analysis Through Hues and Areas (AGATHA) toolkit, and pressure-activated force plates allied to digital interpretation.

The gait analysis and identification step is extremely important. Locomotion patterns are most likely controlled by several genes, each one playing a small part in the control of the CPGs. With increased understanding of the small differences between each pattern, we can better link the genetic differences underlying these patterns.

Figure 3. Lameness Locator™, a wireless motion analysis system that uses sensors to detect asymmetries in gait, being utilized to evaluate lameness in a horse at the University of Florida.
Credits: UF/IFAS

Currently, genetic testing for the *DMRT3* gene is commercially available to the horse owner. Commonly known as SynchroGait™, this test can be used for genetic assisted selection by breeders who want to alter the performance of their horses in transitions and at the canter. The test is particularly useful for selection of horses that must avoid transitioning to canter (breaking gait) at high speeds, as in pacing or trotting competitions.

Genetic tests detecting the variant in the *DMRT3* gene are the first step in using genomic technology to select horses with the desired complex locomotor patterns. Nevertheless, more research is needed, especially when we consider the remarkable diversity of four-beat locomotion patterns performed by the many gaited breeds. Such genetic research is costly, and it will likely require assistance from organizations that can benefit from use of these tools.

Through continued research, researchers might be able to discover many useful genetic components controlling locomotion patterns specific to each breed of horse. The development of selection tools will allow breeders, trainers, and owners to more accurately select and breed horses. These tools will also assist individuals in designing specific training protocols that can enhance marketability and performance of the horses. Moreover, findings from this area of research may also provide insights into the fundamental biology leading to locomotion variation in all vertebrates.

Glossary of Terms

Allele: alternative form of a gene found at the same place on a chromosome.

Chromosomes: threadlike bodies that carry the genes in a linear order.

Gene: a distinct sequence of nucleotides forming a unit of heredity that can be transferred from a parent to offspring and is held to determine some characteristic of the offspring.

Genotype: the genetic constitution of an individual organism.

Heterozygous: a genotype consisting of two different alleles at a given locus.

Homozygous: a genotype consisting of two identical alleles at a given locus.

Locus (Loci): the position of a gene on a chromosome.

Phenotype: the set of observable characteristics of an individual resulting from the interaction of its genotype with the environment.

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