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The potential role of the muscle in kinematic characteristics

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Summary

This review describes characteristics of equine skeletal muscle fibre types in relation with their potential role in kinematics characteristics. Equine skeletal muscles are composed by fibres with different metabolic and contractile properties. Histochemical fibre typing has proven useful in numerous studies in horses concerned with structure-function relationships. More recently, immunohistochemical and electrophoretic methods have established a relationship between histochemical fibre types and their myosin heavy chain content. Muscle is a tissue which displays a great deal of plasticity, in that it can generally adapt to the varying demands placed on it. Several studies suggest that not only hereditary factors are significant but that certain environmental stimuli are also important in the establishment of the fibre type composition of equine muscle. Some other studies justify the attempt to select (or reject) horses using muscle fibre type composition as a criterion. In 30 young Andalusian horses exercised in a working trot, a significant negative correlation was seen between the duration of the stance phase of the stride and diameter of fibre types. Conversely, the stride frequency was correlated positively with the fibre sizes. These correlations indicate that the locomotor pattern of the horse may be partly dependent on muscle fibre properties.

Keywords: skeletal muscle, locomotion, muscle fibres, myosin heavy chain, horses

Die potentielle Rolle des Skelettmuskels im Rahmen der Charakteristika der Bewegung

In dieser Übersicht werden die Merkmale der verschiedenen Fasertypen der Skelettmuskulatur von Pferden im Zusammenhang mit ihrer möglichen Rolle bei verschiedenen Bewegungsabläufen beschrieben.
Der Skelettmuskel des Pferdes setzt sich aus Fasern mit verschiedenen metabolischen und kontraktilen Eigenschaften zusammen. Die histochemische Fasertypbestimmung hat sich in vielen Untersuchungen an Pferden, die den Zusammenhang zwischen Struktur und Funktion zum Gegenstand haben, als nützlich erwiesen. In letzter Zeit wurde durch immunohistochemische und elektrophoretische Methoden ein Zusammenhang zwischen den histochemisch bestimmten Fasertypen und ihrem Gehalt an schweren Myosinketten aufgezeigt. Der Muskel ist ein Gewebe mit großer Veränderungsfähigkeit in dem Sinne, daß er sich an die verschiedensten Anforderungen anpassen kann. Viele Studien geben Hinweise darauf, daß nicht nur erbliche Faktoren, sondern auch bestimmte Reize aus der Umwelt eine wichtige Rolle für die Zusammensetzung des Muskels aus verschiedenen Fasertypen spielen. Andere Studien rechtfertigen den Ansatz, die Muskelfaserzusammensetzung als Selektionskriterium für Pferde einzusetzen.
Bei 30 jungen Andalusischen Pferden, die einer Trabbelastung unterzogen wurden, bestand eine signifikante negative Korrelation zwischen der Dauer des Auffußens und dem Durchmesser der Muskelfasern. Die Schrittfrequenz hingegen war mit der Fasergröße positiv korreliert. Diese Korrelationen weisen darauf hin, daß das Bewegungsmuster des Pferdes zum Teil von der Muskelfaserzusammensetzung abhängig sein könnte.

Schlüsselwörter: Skelettmuskel, Lokomotion, Muskelfasern, schwere Myosinketten, Pferde

Introduction

Speed is a product of stride length and stride rate (*Gunn* 1983). Both of these are dependent on a number of factors, many of which are related to certain muscle properties. Thus, stride length is dependent on both the acceleration capacity (or force produced by muscles relative to body weight) and the arrangement of muscle fibres within the muscles. Likewise, stride frequency is a function of the mechanical advantage of muscles, intrinsic speed of sarcomere contraction and repetitivity of limb movements (aerobic and anaerobic energy supply mechanisms). Although two recent studies have shown a significant relationship between muscle characteristics and kinematic variables in trotters (*Persson* et al. 1991; *Ronéus* et al. 1995), our knowledge about this relationship is still limited.

During locomotion energy is used to move the horse's centre of gravity from place to place, and to protract and retract the limbs during every stride. Locomotor muscles in the horse are strategically located proximally on the skeleton, which reduces the weight of the lower limb, thereby decreasing the energy necessary to overcome inertia when the limb swings back and forth (*Snow* and *Valberg* 1994). The limb functions as a driven pendulum. Movements of the distal limb are mainly passive, as a result of the release of elastic energy from the flexor tendons and suspensory ligament as the limb is unloaded. Movements of the proximal limb are brought about by active muscular contraction (*Jansen* et al 1992). It has been suggested that physiological factors, such as force-velocity characteristics of muscle, nerve conduction velocities and the proportion of fast twitch muscle fibres may play a role in limiting stride frequency (*Mero* et al. 1981).

One unique characteristic of skeletal muscle is its diversity. This diversity is created by its design, i.e. its fibre composition and the heterogeneity of the individual fibres. Such heterogeneity of muscle tissue reflects its high degree of functional specialisation and is the basis of its functional plasticity. Over the last two decades numerous studies have been published describing muscle characteristics in horses, showing that equine skeletal muscle is essentially similar to all mammalian muscles (see *Snow* and *Valberg* 1994 for a review). However, we must progress beyond our descriptive muscular studies, explore further the muscular properties of the equine athlete and integrate this information with that obtained from other sport science disciplines. The aim of this review is to summarise and integrate our current knowledge of the qualitative and quantitative differences among equine skeletal muscle fibres at the level of cellular and molecular organisation, and to discuss how this cellular and molecular diversity of muscle fibres may contribute to explaining the gait quality of the horse.

Percutaneous muscle biopsy

In horses, specimens satisfactory for histochemical, immunohistochemical, biochemical and structural studies can be obtained percutaneously by a special biopsy needle *(Lindholm* and *Piehl* 1974). This method is extensively used because of its ease, safety and relatively atraumatic nature, allowing repeated sampling during and following exercise bouts without any adverse effect on performance. The author has removed thousands of biopsies from the gluteus medius muscle, a major propulsive muscle of the hind limb and very active in locomotion, with negligible untoward effect.

Muscle fibre type

Mammalian skeletal muscles are composed of a mixture of different fibre types with varying metabolic and contractile properties. Although only a small number of major fibre types can be discriminated by qualitative histochemical methods, histochemical fibre typing has proven useful in numerous studies in horses concerned with structure-function relationships in both normal and pathological muscles *(Snow* and *Valberg* 1994). In horses, as in other mammals, muscle fibres have been routinely categorised into three major types, designated types I, IIA and IIB, and the minor IIC, based upon the myofibrillar actomyosin adenosine triphosphatase (mATPase) histochemical reaction proposed by *Brooke* and *Kaiser* (1970). In addition to these four fibre types, some fibres with staining characteristics intermediate between types IIA and IIB (type IIAB) have frequently been observed in horses *(Rivero* et al. 1993).

Using immunohistochemical and electrophoretic methods, it has been suggested that the histochemical staining intensity of the mATPase reaction in a given muscle fibre is determined by its myosin heavy chain (MyHC) content. Myosin is the primary protein in the thick myofilament, and its molecule is formed by two identical MyHCs and four myosin light-chains. To date, four distinct MyHC isoforms have been identified in adult skeletal muscles of a number of species *(Pette* and *Staron* 1990). However, the horse only has three of these four MyHC isoforms: one slow or type I and two fast termed type IIa and type IIb. The differential distribution of these MyHCs defines three major fibre types, each containing a single MyHC (types I, IIA and IIB) and two intermediate hybrid fibre populations containing either slow and fast IIa-MyHCs (type IIC fibres) or the two fast, MyHCs (type IIAB fibres) *(Rivero, Talmadge* and *Edgerton* 1995, unpublished data).

Histochemical, immunohistochemical and electrophoretic techniques applied to equine skeletal muscle have recently established a relationship between qualitative mATPase activity and MyHC content of muscle fibres *(Rivero, Talmadge* and *Edgerton* 1995, unpublished data). However, a high percentage of fibres of the equine gluteus medius muscle are mis-classified by traditional mATPase histochemistry, since it does not adequately identify the hybrid fibre population coexpressing the two fast MyHC isoforms. Many fibres histochemically identified as type IIB displayed both type IIa and type IIb MyHC isoforms, and nearly all type IIAB fibres in mATPase contained only the type IIa MyHC isoform by immunohistochemistry. Therefore, despite the extensive use of mATPase histochemistry to distinguish skeletal muscle fibre types in horses, these findings do not support the use of this qualitative technique. The use of monoclonal antibodies against specific raised MyHCs seems to be a more sensitive, more reproducible and less subjective method for that purpose.

Characteristics of equine muscle fibre types

Muscle fibres differ in maximum velocity of shortening (V_{max}), and it is thought that recruiting fibre types with different V_{max}s enables animals to generate force and power efficiently over their full range of movements. Physiologically, type I and type II fibres have been shown to be relatively slow and fast contracting, respectively, and therefore are also referred to as slow- and fast-twitch fibres. In addition, type IIA fibres have a slower V_{max} than type IIB fibres *(Rome* et al. 1990). The variation in V_{max} within the type IIAB group is related to the proportion of IIa and IIb MyHCs *(Pette* and *Staron* 1990). It was first predicted by *Hill* (1950) that (a) as body size increases, the velocity of shortening of the muscles (V) decreases and (b) to keep the mechanical and energy properties of muscle matched to function, V_{max} should decrease by the same proportion (i.e. so that V/V_{max} remains constant). Hill's model predicts, for instance, a 10-fold difference in V_{max} between rat and horse muscle. In the horse, there is a 10-fold difference in mean V_{max} between the three histochemical fibre types *(Rome* et al. 1990). Conversely, in small animals only a three- to fivefold difference in V_{max} between fibre types is seen. In other words, comparison of V_{max} over a 1200-fold range (450 kg horse vs. 0.38 kg rat) of body mass suggests that type I fibres scale more dramatically than do fast IIB fibres. This means that equine type IIB fibres shorten more rapidly than would be expected from normal scaling, and also this difference may enable the slow type I fibres to work at high efficiencies in the large animal while the fast type IIB fibres can still generate a large mechanical power when necessary.

For the assessment of oxidative capacity, fibres are incubated for determination of either succinic dehydrogenase (SDH) or NADH-tetrazolium reductase activity and classed as having either high or low activity. The quantitative histochemical determination of single fibre SDH activity has also been used in horses *(Rivero, Talmadge* and *Edgerton* 1995, unpublished data). Despite the overlap in the distribution of SDH activities among fibre types, significant variations were recorded for the overall population among fibre types, with type I fibres being more oxidative than fast fibres. Within the fast fibres, the order of oxidative capacity is type IIA>type IIAB>type IIB. The oxidative differences shown histochemically have also been supported by biochemical studies on pools of single fibres *(Valberg* and *Essén-Gustavsson* 1987).

Fibre sizes also can be determined from histochemical preparations. Despite the overlap in the distributions of cross-sectional areas among the four fibre types, significant differences among fibre types have been observed *(Snow* and *Valberg* 1994). Thus, the fibre size is in the order IIB>IIAB> IIA>I. Fibre size correlates with force output by muscle. In the horse, force output is more important to strength and sprinting events than to endurance events; the explosive nature of the acceleration required for these

activities demands the recruitment of larger fibres (type IIB). Conversely, in endurance exercises, smaller fibres with high oxidative potential assume a much greater importance; because there is a correlation between cross-sectional area and oxygen diffusion time, the supply of both oxygen and nutrients is faster and more efficient in these fibres.
Histochemical stains also have been used to show other differences between fibre types. Using the α-amylase-PAS reaction, capillary density has been found to be highest in the most highly oxidative fibres (I>IIA>IIAB>IIB) *(Rivero* et al. 1995)

Muscle recruitment

For coordinated locomotion, muscles are recruited in an orderly manner, with both extensors and flexors being involved during each stride cycle *(Snow* and *Valberg* 1994). Within a particular muscle, only certain portions may operate, having different and often complex functions due to functional compartmentalisation. Even within a recruited muscle not all fibres are stimulated, since it is not generally necessary for a muscle to generate maximum tension. Muscle fibres are selectively recruited in a specific pattern that varies according to the gait, speed, and duration of exercise. This occurs through the differential stimulation of α-motor neurones. The smallest-diameter motor neurones which have the lowest threshold innervate type I fibres, while the largest innervate type IIB fibres. For the maintenance of posture and for exercise at low speeds, it is only generally necessary to recruit type I fibres, which are fatigue-resistant. As the speed of movement increases, the development of more tension to generate the required torque is necessary, and type IIA fibres are recruited. The very forceful contractions of high speeds or for jumping result in the additional recruitment of first the type IIB oxidative and then the low oxidative fibres.

Plasticity of equine skeletal muscle and relation to performance

Muscle is a tissue which displays a great deal of plasticity, in that it can generally adapt to the varying demands placed on it. Over the past two decades, great interest has been shown in factors affecting histochemical properties of equine skeletal muscle. Now, there is sufficient evidence that certain muscle characteristics vary in a number of ways: breed, age, sex, training, anatomical and pathological aspects, etc. (see *Snow* and *Valberg* 1994 for a review). Inheritance of the fibre type composition and the influence of training on this have been extensively studied in locomotor muscles of laboratory animals and man *(Komi* and *Karlsson* 1979; *Nimmo* and *Snow* 1983). The proportion of type I and type II fibres shows a high heritability value implying a marked genetic influence. Numerous studies have been published which describe muscular adaptation in response to increased physical activity. The oxidative capacity and number of capillaries of muscle fibres are mainly increased, but the type I/ type II fibre ratio can also be changed depending on training intensity and duration and animal age *(Snow* and *Valberg* 1994). Such studies suggest that it is not only hereditary factors that are significant determinants but that certain environmental stimuli are also important in the establishment of the metabolic profile and fibre type composition of equine skeletal muscle.
In horses, differences in fibre types between individuals also have a genetic as well as a phenotypic basis. There have been many studies of the relationship between the performance capacity and muscle characteristics of horses *(Snow* and *Valberg* 1994 for a review). Some of these reports have shown that the performance of racehorses was related to the muscle fibre type composition of certain muscles. In endurance horses, it has been found that the horses with the best performance records have a higher percentage of types I and IIA fibres, a lower percentage of IIB fibres and larger type I and IIA fibres than horses considered as moderate or poor performers *(Rivero* et al. 1993). These differences indicate a functional adaptation of the muscle that may be related partly to training factors and partly to genetics. But as all the horses in that study had been trained in a similar way, it is reasonable to assume that some of the difference in muscle characteristics may have been related to inherent traits.
These genetically based differences have raised the possibility of whether at an early age, prior to purchase and training, a muscle biopsy will allow selection of horses suited for a particular type of competition. In a parallel study *Rivero* (1996) has found that an optimal discrimination between endurance horses with different performance records is possible by applying multivariate statistical procedures that take into account the overall information derived from multiple gluteus medius muscle biopsies. Therefore, the preceding finding does justify the attempt to select horses using muscle fibre composition as one criterion. However, it has to be realised that successful performance is dependent on interaction between many genetic and training factors. Thus finding a horse with the desired fibre composition is no guarantee of success; rather, it improves the chances. Assessment of fibre composition is probably of great value in eliminating horses with an undesirable proportion of a particular fibre type.

Relation between muscle characteristics and kinematics

In a recent study by *Persson* et al. (1991) locomotion pattern (expressed as stride length and stride frequency) was correlated with muscle fibre composition and enzyme activities in 30 Standardbred trotters exercised on an inclined treadmill at V_{200} (velocity producing a heart rate of 200 bpm). Stride length was significantly correlated to the percentages of type I ($P<0.05$) and type IIA fibres ($P<0.001$) and inversely on the percentage of IIB fibres ($P<0.001$), whereas stride frequency was only correlated significantly with the percentage of the type IIA fibres ($P<0.05$). These findings seem to suggest that longer strides are primarily achieved by recruitment of type IIA fibres which are dependent on aerobic energy release *(Valberg* and *Essén-Gustavsson* 1987). The fact that one particular training effect is a conversion of IIB fibres into type IIA *(Snow* and *Valberg* 1994) seems to indicate that longer strides may be facilitated, which could imply an improvement in racing performance (*Heglund* and *Taylor* 1988). Thus, stride length seems to be the primary determinant of both velocity and aerobic energy expenditure, both of which were shown to be related to the fibre type composition in Standardbreds during treadmill trotting at the lactate threshold *(Persson* et al. 1991).
In another recent investigation a significant negative correlation was seen between the percentage of type IIB fibres and stance time ($r=-0.78$) in young Standardbred trotters during maximal exercise on a track *(Ronéus* et al. 1995). In other words, those horses with a high percentage of type IIB fibres can perform maximal trotting with a short duration of the stance phase. The stance is the phase of the stride when the horse's limb is in contact with the ground and subsequently the phase in which the horse can propel the body forward (*Clayton* 1989). Consequently, the power developed by muscles should be greatest during this phase.

Tab. 1: Descriptive statistics for stride characteristics during working trot and skeletal muscle properties at two different depths from the gluteus medius muscle in thirty 4-year-old Andalusian horses

	Mean	SD	Min	Max
Stride characteristics				
Velocity (m/s)	3.68	0.33	3.06	4.52
Stance phase (s)	0.5	0.04	0.44	0.58
Swing phase (s)	0.137	0.02	0.1	0.18
Stride length (m)	2.30	0.18	1.93	2.79
Stride frequency (stride/s)	1.585	0.1	1.4	1.77
Muscle characteristics: Superficial region of the muscle (2 cm)				
Percentages				
I	20	6	11	37
IIA	37	6	27	58
IIB	43	6	24	56
Diameter (µm)				
I	46	8	35	63
IIA	54	10	41	74
IIB	65	9	50	85
Muscle characteristics: Deep region of the muscle (6 cm)				
Percentages				
I	33	11	17	63
IIA	41	6	31	55
IIB	26	11	0	44
Diameter (µm)				
I	48	7	37	60
IIA	54	8	39	65
IIB	60	8	48	78

The authors have compared kinematic variables versus percentages and diameters of fibre types at two different depths of the gluteus medius muscle in 30 young Andalusian horses exercised in a working trot. Mean values and descriptive statistics of all variables are shown in Table 1. The percentage of type I fibres was higher and that of type IIB fibres was lower (P<0.001 in both) in the deep region of the muscle compared with the superficial region. A significant negative correlation was seen between the duration of the stance phase of the stride and diameter of fibre types (Tab. 2 and Fig. 1). Conversely, the stride frequency was correlated positively with the fibre sizes. Correlation coefficients were higher for type I and IIA fibres than for type IIB fibres, and in the superficial region of the muscle compared with the deep region. Because these animals were trotted at a relatively low speed (3.68±0.33 m/s), there is mainly a reliance on aerobic metabolism for energy release and recruitment of type I and IIA fibres which have a high oxidative capacity. The higher coefficients of correlation seen in the superficial region in comparison to the deep region of the muscle probably indicate that there are functional differences between the various parts of the muscle. The deeper portions have a more postural role, while the more superficial portions are recruited with increasing work loads (*López-Rivero* et al. 1992). The negative correlation between fibre diameters and stance time might be explained by the fact that the propulsive forces of the muscles act when the feet are in contact with the ground so the horse's ability to propel itself forwards should be greater in animals with large fibres, since the force generated by a given muscle fibre is directly proportional to its diameter (*Hill* 1950). The total force exerted also depends on the duration of the stance phase. When stride rate decreases, the stance phase decreases, necessitating the application of a higher force over a shorter time to maintain the overall force production. This may explain the ability of horses with larger diameter fibres to perform at higher stride rates.

Conclusions

Correlations between kinematic variables and muscle properties indicate that the locomotor pattern of the horse may be partly dependent on muscle fibre composition, metabolic profile of the muscle and muscle fibre size. To date our knowledge of muscle physiology in horses is almost equal to that in humans and some laboratory animals. The individual differences in muscle characteristics in horses are attributed to a main genetic effect, an average non-genetic effect (e.g. training, nutrition) and the unpredictable interaction of training and genotype. Muscle biopsy may be a use-

Tab. 2: Speed and locomotor pattern relationships with percentages and diameters of fibre types

	Percentages			Diameters		
	I	IIA	IIB	I	IIA	IIB
Superficial region of the muscle (2 cm)						
Stance phase (s)	-0.10	0.08	0.02	-0.61***	-0.58***	-0.45*
Stride frequency (stride/s)	0.07	-0.08	-0.35*	0.63***	0.64***	0.40*
Deep region of the muscle (6 cm)						
Stance phase (s)	0.02	0.01	-0.02	-0.63***	-0.44*	-0.18
Stride frequency (stride/s)	0.05	-0.01	-0.12	0.64***	0.38*	0.18

* P<0.05; *** P<0.001

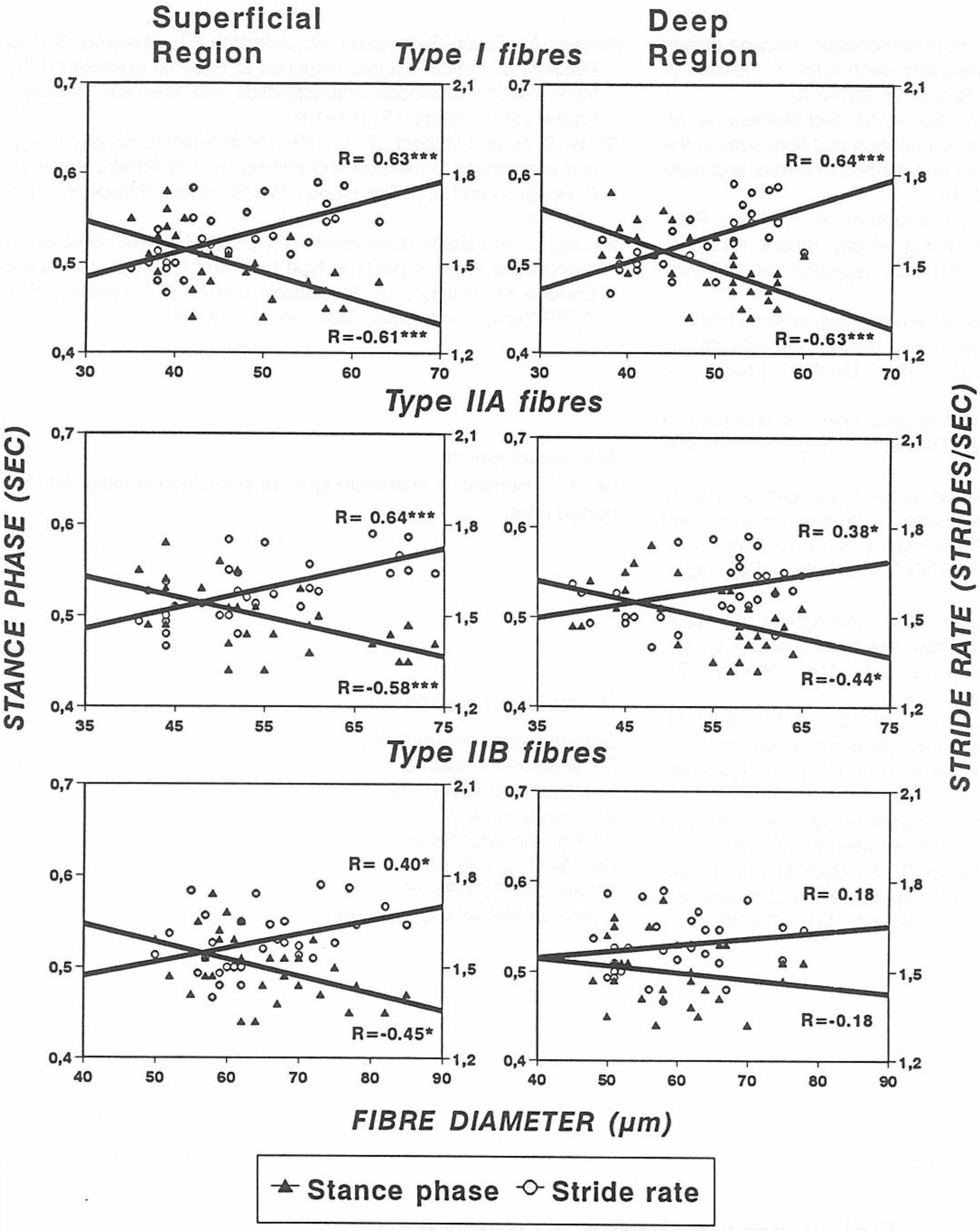

Fig. 1: Lesser fibre diameter of fibre types (µm) at two different depths of the gluteus medius muscle in relation to stance phase (sec) and stride rate (stride/sec) during working trott (3.68$±0.33 m/sec) in thirty 4-year-old Andalusian stallions.
*, **, *** Correlation coefficients (R) are statistically significant at P<0.05, P<0.01, and P<0.001, respectively

ful aid for estimating physical ability, performance and adaptation to training in horses.

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