

The horse and dog, elite athletes—why and how?

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It is the purpose of this paper to outline some of the adaptations which have allowed both the dog and horse to become well adapted to undertake either sprint or prolonged exercise, and contrast these to findings in man. To keep within the theme of this symposium, factors will be discussed that can be considered responsible for the maintenance of adequate turnover of ATP to permit work to continue at the desired intensity. Therefore, the capacities of the cardiovascular, muscular and thermoregulatory systems will be considered. Further details and references on the first two systems can be obtained from a recent paper by Snow & Harris (1984).

That these two species have evolved as having elite athletic prowess has been brought about largely by their domestication and their selection for specific tasks initially connected with hunting, farming and warfare, and more recently for leisure activities. Within the canine species, the greyhound is the fastest breed, attaining speeds just under 1000 m/min over 400 m. This breed has evolved over 5000 years originating in Babylon and Egypt, with reference to its participation in coursing being recorded in Ancient Rome by Ovid. The continual development for speeds with stamina has led to the modern greyhound, which is little changed from the excellent description given over 100 years ago by Dalziel (1868). 'He is a combination of art and nature that challenges the world unequalled in speed, spirit and perseverance, and in elegance and beauty of form as far removed from many of his clumsy ancestors as the English thoroughbred from a coarse drayhorse'. At the other end of the canine spectrum are the sled dogs (huskies) which can race over distances up to 1710 km in 12–14 d.

In comparison to the dog, in the horse development for true speed is of much more recent occurrence. The thoroughbred which is portrayed as the epitome of speed has only been developed within the last 300 years, evolving from hot-blooded types such as the Arab. Within the thoroughbred more and more speed has been selected for, as races became shorter, largely from this breed has occurred the development of the American racing quarterhorse, an animal that can attain speeds of 1200 m/min over 400 m.

The eliteness of these two species is well illustrated when maximal oxygen consumptions are studied, as even non-elite members of these species have higher than predicted values (Taylor *et al.* 1981). Members of both species have maximum O₂ consumption in excess of 100 ml/kg per min. The high aerobic capacity indicates a very high metabolic activity of working muscle, and must be related to adaptations within both the cardiovascular and muscular systems.

Cardiovascular system

Within the cardiovascular system the ability to transport large quantities of O₂ to working muscle has occurred in a number of ways. In contrast to man the elite athletic breeds of both species are able to increase markedly the number of circulating erythrocytes due to the spleen acting as a reservoir. During maximal exercise the packed cell volume can attain values of between 0.60 and 0.70 litres/litre (Snow & Harris, 1984). In conjunction with a marked increase in cardiac output this permits a very large increase in blood flow to the working muscle. Even in ponies, blood flows as high as 155 ml/min per 100 g muscle are reached (Parks & Manohar, 1983), compared with a value of approximately 60 ml/min per 100 g in man. The marked increase in cardiac output is largely due to the very high heart rates that can be attained in the horse and dog. In the fit thoroughbred, resting heart rates in the mid twenties occur, whilst during maximal exercise the heart rate can be as high as 240–250 beats/min. In the dog, resting heart rates can be less than 100, rising to 300 beats/min during maximal exercise. A high cardiac output is also aided in the elite of each species, as they have high heart weight: body-weight values (g/kg). In the thoroughbred the mean value is 8.6 (Stewart & Steel, 1970), in the greyhound 12.0 (Steel *et al.* 1976), whilst in man it is in the order of 4.0 (Keele *et al.* 1982). Within these elite breeds, the best performing animals may possess considerably greater values than these mean values.

Muscular system

When this system is examined adaptations can be seen to have occurred at the gross, microscopic and biochemical levels. In the greyhound, it has been reported that muscle relative to live weight is 57%, a value that the investigator (Gunn, 1978*a*) considered unique for terrestrial mammals, and considerably in excess of the 40% found in most mammals studied. Unfortunately similar values have not been obtained for racehorses, although it has been shown that as in the greyhound, in the thoroughbred the proportion of muscle in the femoral region is greater than that in other breeds of the respective species. This greater mass around the hip joint favours a high natural frequency of hind-limb movement facilitating a high stride frequency (Gunn, 1983). Gunn (1978*b*) has reported that this greater muscle mass may be explained by both greater cell number and fibre area. Although these specific breeds do have a greater fibre area than non-elite athletic breeds, it is interesting to note that in the dog, fibre areas are relatively small, being of a similar size to the cat. The relatively small size of canine muscle fibres may be related to the high oxidative capacity of all fibres. This establishes a high surface area: volume allowing a rapid diffusion of O₂.

Using conventional histochemical methods, equine muscle fibres can be separated into the three basic types seen in other species. A combination of metabolic and contractile indicators identifies three fibre types, slow twitch (type I) and high- and low-oxidative fast twitch (type II) fibres, whilst determination of myosin ATPase activity after acid pre-incubation results in the identification of

type I, IIA and IIB fibres. In the canine, although both type I and type II fibres can be identified, all type II fibres are both high oxidative and high glycolytic. Using enzyme histochemistry, immunocytochemistry for myosins and peptide mapping of myosin heavy chains, it has been shown by Snow *et al.* (1982) that although the typical type IIA fibre exists, a sub-type which differs from the normal type IIB (perhaps to be called type IID) also exists. The physiological significance of possessing this special type II fibre is unknown, but it may be associated with all type II fibres being fatigue resistant as shown by Maxwell *et al.* (1977), therefore aiding in bestowing both speed and stamina when all fibres are recruited. As power output and speed are generally associated with fibres of large cross-sectional areas, which the dog does not possess, it is possible that the ability to develop power is related to its ability to sustain force output by a continuous recruitment of numerous fatigue-resistant fibres.

Between breeds of both species differences in the fibre composition of limb muscles can be seen, and these can be related to performance characteristics for which the particular breed has been selected for (Snow & Guy, 1980; Snow, 1983; Guy & Snow, 1981). In the horse this difference is most prominent in the middle gluteal, one of the largest muscles, and important for the generation of propulsive forces. In the horse, as well as differences in the proportion of type I and type II fibres, variations between and within breeds can also be seen in fibre areas, and oxidative capacity, which probably have both genetic and environment (training) components (Snow & Guy, 1981).

When the greyhound is compared with other canine breeds, the influence of selection over thousands of years is best seen. In six limb muscles studied by Guy & Snow (1981), an almost complete predominance of type II fibres throughout the depth of the muscle was found. Studies also indicated that in the greyhound the majority of fibres are of the atypical type II.

When the importance of metabolic pathways are examined, it can be seen that compared to man, both horse and dog would appear to be able to produce higher blood lactates associated with either single or repeated bouts of supramaximal exercise (Snow & Harris, 1984). This is also supported by the findings of muscle lactate concentrations in thoroughbred horses reaching as high as 53 mmol/kg wet muscle after intermittent exercise and 36 mmol/kg wet muscle after a single exercise, which is considerably in excess of levels reported in man. Despite this ability to accumulate high concentrations of lactate, the buffering capacity of both equine and human muscle is similar.

When enzyme activities (e.g. phosphorylase (*EC* 2.4.1.1), phosphofructokinase (*EC* 2.7.1.11), lactic dehydrogenase (*EC* 1.1.1.27), alanine aminotransferase (*EC* 2.6.1.3) connected to anaerobic metabolism are examined, the higher anaerobic capacity of thoroughbred and greyhound muscle are borne out (Snow & Harris, 1984). Even within species breed differences are seen. When glycolytic capacity is examined, the glycogen content of human and equine muscle is fairly similar, whilst interestingly it is considerably lower in the dog. This may be a reflection of

the normally higher protein content of the canine diet than seen in the other species.

A recent interesting finding in line with the high anaerobic capacity of the thoroughbred is that a considerable reduction of ATP occurs with supramaximal exercise. These decreases in ATP have been seen with both repeated (Snow *et al.* 1985) and single bouts of exercise, and are much greater than the small decreases that have been occasionally reported in man. Associated with the decrease in ATP is a large increase in inosine monophosphate (IMP) and other degradative products. The reasons for and relationship to fatigue of this large loss of ATP are currently under investigation by studying the activities of enzymes involved in purine metabolism. So far we have found that in the horse and dog, AMP deaminase (*EC* 3.5.4.6) activities are higher than in the rat (Snow & Harris, 1984) and in the horse increase with training.

In examining the oxidative capacity of muscle fibres in horses and dogs it is generally found that enzyme activities are higher than those reported in man, e.g. oxoglutarate dehydrogenase (*EC* 1.2.4.2) (Snow & Harris, 1984). In parallel with the high oxidative metabolism is also a high ability to utilize free fatty acids as indicated by a high 3-hydroxyacyl CoA dehydrogenase (*EC* 1.1.1.35; HAD) activity. Surprisingly it appears that even the greyhound has a greater HAD activity than man, although this animal is thought to place little reliance on fat stores, being found to have a very low body fat composition. An area worthy of investigation is fat metabolism in the husky, as they have great endurance and are maintained on a high-fat, high-protein, low-carbohydrate diet (their natural diet being seal meat). Interestingly it has been shown that the best performance of huskies occurs on a diet with less than 10 g carbohydrate/kg, and on high-carbohydrate diets medical problems are encountered (Kronfeld, 1973; Hammel *et al.* 1977).

Thermoregulation

The foregoing sections have illustrated the ability to attain very high metabolic activities during exercise. Obviously associated with this high production of ATP and muscular contractions, is the generation of large amounts of heat which have to be dissipated from the body. In the dog the major means of heat dissipation is via the respiratory tract and the mechanisms of panting, where approximately 60% of heat loss occurs during hard work (Young *et al.* 1959). On the other hand in the horse heat loss occurs mainly via sweating and therefore a similarity exists to man. In the horse sweating is adrenergically mediated via β_2 -adrenoceptors (Snow, 1977) and exercise-induced sweating involves both sympathetic nervous system activity and circulating adrenaline whilst heat-induced sweating is controlled entirely by the sympathetic nervous system without adrenomedullary involvement (Robertshaw & Taylor, 1969). Although sweating is the major thermoregulatory mechanism in both man and horse, the composition of the sweat differs (Table 1). Equine sweat is hypertonic for most ions, and for the major ions the concentration is maintained throughout sweating (Kerr & Snow, 1983), whilst

Table 1. Concentration (mmol/l) of major electrolytes in sweat

	Sodium	Potassium	Chloride
Plasma	140	3.5-4.5	100
Human sweat	10-60	4.0-5.0	10-60
Equine sweat	130-190	20-50	160-190

with time there is a reduction in calcium and magnesium concentration. The hypertonicity of equine sweat would suggest that no reabsorption of electrolytes occurs in the neck of the gland as seen in man. This hypertonicity does mean that electrolyte losses can be more significant in the exercising horse than man, especially as the horse's diet is low in sodium.

One extremely interesting aspect of equine sweat is that it has a high protein composition, values up to 20 g/l being reported (Kerr & Snow, 1983). It was originally suggested that this high protein content may be an important source of protein loss to the animal. However, studies by Kerr & Snow (1983) have shown that in parallel with Mg, as sweating continues, there is a decline in protein concentration to 1 g/l or less. Contrary to earlier beliefs that this protein was mainly albumin, studies by Eckersall *et al.* (1982, 1984) have now shown that it mainly consists of two glycoproteins of relative molecular weights 49 000 and 33 000. As both these glycoproteins have low levels of sulphur-containing amino acids and histidine, we have speculated that they may act as surfactants, aiding the dispersion of sweat droplets along the coat, thus favouring a more rapid evaporative loss. These proteins are considered to be stored within vesicles in the sweat gland cells, as the vesicle numbers can be seen to decrease during sweating (Montgomery *et al.* 1982).

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