Factors affecting oxygen consumption in the horse

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Sammanfattning

Hästen utmärker sig som en suverän atlet jämfört med andra arter och en av de viktigaste faktorerna som påverkar hästens fysiska prestationsförmåga är syreupptaget. Många av de fysiologiska parametrar som är inblandade i syreupptag ökar väsentligt under ansträngning. Tömning av mjältens reserv orsakar upp till en dubblering av antalet röda blodkroppar som tillsammans med bland annat en sjufaldig ökning av hjärtfrekvensen bidrar till att transportera syret till musklerna. Andningsfrekvensen kan öka tiofalt och tidalvolymen mer än dubblas jämfört med motsvarande värden under vila.

Det finns även effekter som på lång sikt kan påverka syreupptaget. Träning minskar hjärtfrekvensen under ansträngning samt ökar hematokriten och hemoglobinets syreaffinitet. Det går att påverka syreupptaget med hjälp av utfodringen. Användningen av socker och fett som alternativ till stärkelse för att höja energitätheten i den högpresterande hästens foder ger återverkningar på syreupptagningsförmågan. Syftet med den här litteraturstudien är att sammanfatta en del av den kunskap som finns om faktorer som påverkar syreupptaget sam belysa lite av vad som återstår att ta reda på.

Abstract

The horse stands out as a supreme athlete when compared to other species. One of the major factors affecting physical performance is oxygen consumption. Many of the physiological parameters involved in oxygen consumption increase dramatically during exercise. Emptying of the spleenic reserve causes up to almost a doubling of the amount of erythrocytes in the blood that together with a seven-fold increase in heart rate among other things contributes to oxygen transport to the muscles. The respiratory frequency can increase ten-fold and the tidal volume more than double compared to resting values.

Abbreviations used in this article:

TBs = Thoroughbreds
STBs = Standardbreds
BW = body weight
V_T = tidal volume
f_R = respiratory frequency
V_E = minute ventilation
RER = respiratory exchange ratio
HR = heart rate
Q_T = cardiac output
VO_2 = rate of oxygen consumption

There are achievable long-term effects on oxygen consumption as well. Training causes a lowering of the heart rate during exercise, an increase in hematocrit and an increase in the oxygen affinity of the hemoglobin. Feeding regimes can alter oxygen consumption. Oxygen consumption is influenced by which energy source that is used to obtain a sufficient energy density in the feed of the high-performing horse. Fat and sugar can be used to replace starch in the ration. The aim of this review is to summarize a part of the knowledge about factors affecting oxygen consumption and also to shed light on some of the things that still remain unknown.

Introduction

As the number of machines used in the military and for agricultural purposes grew after the 2nd world war, the use of horses as transportation and draft power rapidly decreased. Today however, horses are gaining in popularity but now a majority of them are used for recreation and sports. When compared to other animals, as well as humans, the horse stands out as a supreme athlete, capable of speed, power and endurance performances.

When compared to other species of the same size, the horse has an extraordinary aerobic capacity (Hoppeler, 1990) but there is variation between horses (Birlenbach Potard *et al*., 1998; Katz *et al*., 2005). Centuries of selection for horses with certain desired characters and abilities has created a variety of horse types, differing not only on the outside but when it comes to physiology as well. The genetic legacy gives the athletic potential of the horse, management and training determines if that potential is fully utilized.

The aim of this review is to cover things that have been found to influence oxygen consumption such as respiratory and cardiovascular parameters, properties of the skeletal muscles and effects of breed, age, training and feed intake.

The respiratory system

When discussing oxygen consumption the function of the respiratory system is an obvious area to mention. The amount of air that reaches the alveoli per minute along with the total alveolar area exposed to this air is the first determinant of how much oxygen that can be used for physical performance.

The lungs

The lungs make up about 1 % of the body weight (BW) (Lekeux & Art, 1994) and 5 % of the body volume (Sjaastad *et al.*, 2003) in horses. In healthy adult horses the total lung capacity is about 55 liters (Lekeux & Art, 1994) but only parts of the total lung capacity is used during breathing, see figure 1. The tidal volume (V_T) is the term for the volume of air inhaled or exhaled in a normal breath. V_T at rest is 11,1 and 5,9 ml per kg BW for fit Thoroughbreds (TBs) and fit ponies respectively (Katz *et al.*, 2005). V_T increases dramatically as a response to increased workload, 29,5 ml per kg BW has been reported for TBs at maximal exercise (Hörnicke *et al.*, 1987).

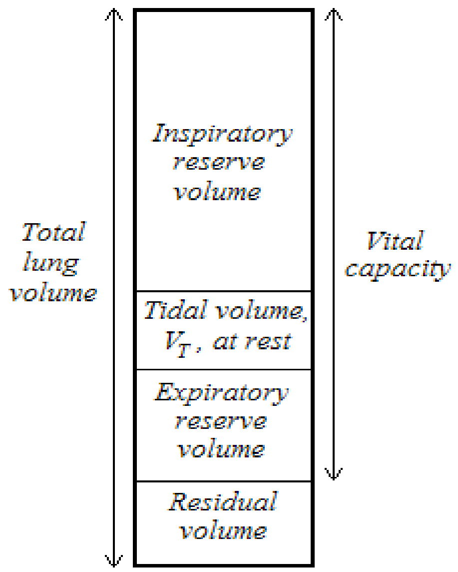

Figure 1. The different lung volumes.

The respiratory frequency (f_R) in a resting horse is on average 8-16 breaths per minute, increasing to a maximum of about 120 breaths per minute due to strenuous exercise (Pilliner & Davies, 2004). The horse has a very strong 1:1 coupling between f_R and stride frequency during gallop (Gillespie, 1990). Questions have been raised on weather there is a limitation of the breathing due to this coupling or, perhaps, a limitation of the stride frequency. This has yet to be determined.

V_T multiplied by f_R equals the minute ventilation (V_E), which reflects the total amount of air inhaled or exhaled per minute. V_E is often expressed either as liters per minute or ml per kg BW and minute. Resting values for V_E is 171,6 and 200,5 ml per kg BW and minute for TBs and ponies respectively (Katz *et al.*, 2005). At the onset of exercise, V_E increases due to an increase in both V_T and f_R (Pelletier *et al.*, 1987b). At fast gallop (a velocity of 805 m per minute), TBs has a f_R of 131 breaths per minute, V_T is 29,5 ml per kg BW and this gives a V_E of 3840 ml per kg BW and minute (Hörnicke *et al.*, 1987).

The inhaled atmospheric air normally consists of about 20 % oxygen, 79 % nitrogen and 1 % carbon dioxide mixed with water vapor. The composition of the exhaled air is only slightly altered with the same concentration of nitrogen but 16 % oxygen and 4 % carbon dioxide and now the air is saturated with water vapor (Pilliner & Davies, 2004). The gas exchange takes place in the alveoli, which are surrounded with pulmonary capillaries. In the adult horse the area of the alveoli and bronchioles is approximately 100 m^2 at the end of expiration and at the end of an inspiration the area has increased three-fold (Art & Lekeux, 2005).

The amount of carbon dioxide produced divided by the amount of oxygen utilized is termed the respiratory exchange ratio (RER) or the respiratory quotient (Eaton, 1994; Sjaastad *et al.*, 2003). RER is different depending on what substrate that has been metabolized. For carbohydrates, RER is 1,0 and for fat and protein RER is 0,7 and 0,8 respectively (Sjaastad *et al.*, 2003). A RER exceeding 1,0 indicates that anaerobic metabolism is producing lactate that is later converted into carbon dioxide (Eaton, 1994).

The cardiovascular system

Once the oxygen is inhaled and has reached the alveoli the cardiovascular system is responsible for transporting it to the mitochondria, where it should be used. The cardiovascular system consists of the heart, blood vessels of different sizes, from the aorta to tiny capillaries, and an important organ for the athletic horse, the spleen.

The heart

The function and capacity of the heart is of vital importance for physical performance. Normal heart rate (HR) in horses at rest is 26-42 beats per minute (Pilliner & Davies, 2004). During maximal exercise HR increases dramatically, values of 240 beats per minute have been recorded (Betros *et al.*, 2002). The amount of blood pumped out of the ventricles in one stroke is termed the stroke volume. Resting values is 2,4 and 3,2 ml per kg BW for TBs and ponies respectively (Katz *et al.*, 2005). The stroke volume increases 20 to 50 % during exercise (Thomas & Fregin, 1981; Evans, 1994).

The cardiac output (Q_T) is the amount of blood pumped out during one minute by each of the ventricles. Q_T is determined by multiplying HR with the stroke volume. Resting values of Q_T is 108,6 and 105,8 ml per kg BW and minute for TBs and ponies respectively (Katz *et al.*, 2005). Fit TBs exercising at maximal rate of oxygen consumption (VO_{2max}) has a Q_T of 789 ml per kg BW and minute (Butler *et al.*, 1991).

The blood

The function of the blood is to transport O_2, CO_2, nutrients, heat and waste products. The total blood volume is correlated to performance level in disciplines where transport of oxygen and waste products is a limitation. Hematocrit is the fraction of the blood volume made up of erythrocytes. During exercise, horses can increase hematocrit due to emptying of the spleen. The maximal hematocrit in adult fit horses is 60-65 %. The spleenic reservoir can contain one-third to half of the total erythrocyte volume (Thomas & Fregin, 1981).

Another determinant of the oxygen uptake is the concentration of hemoglobin in the blood. At spleenic emptying, the concentration of hemoglobin rises along with the hematocrit. The concentration of hemoglobin in the blood for horses at rest is around 100 g per liter (Sexton *et al.*, 1987; Pelletier *et al.*, 1987a) but at strenuous exercise it can reach values of 230-250 g per liter (Evans & Rose, 1988; Butler *et al.*, 1991). Two factors that determines the affinity of hemoglobin for oxygen is pH and temperature. During strenuous exercise the temperature in skeletal muscles can rise to 42-43°C and the pH falls. This leads to increased unloading of oxygen in the capillaries in the skeletal muscles. Because the temperature in the lungs at the same time will change only slightly due to the cooling effect of inhaled air the oxygen uptake will not be affected as much (Sjaastad, 2003).

The skeletal muscles

The skeletal muscle tissue make up to 37-43 % of the body mass of horses. More than 60 % of the muscle mass is located in the hind- and forelimbs and are involved in locomotion (Hoppeler *et al.*, 1987). The muscles consist of connective tissue, blood vessels, nerves and muscle cells. During strenuous exercise, a majority of the blood flow is directed to the skeletal muscles (Sjaastad *et al.*, 2003).

The muscle fibers

Muscle cells are also called muscle fibers and are large cells made up of embryonic muscle cells that are fused. The muscle fiber therefore contains a large number of nuclei. The length of a muscle fiber can be several centimeters and the diameters vary with activity and fiber type. Muscle fibers are divided into two types, I and II, based on their contraction velocity and myosin ATPase activity. Type I has a lower contraction velocity and activity of myosin ATPase than type II. Type II is further divided into sub-types, IIa, IIb and lately also IIx, based on the concentration of oxidative and glycolytic enzymes in the cell. The different types of muscle fibers also have other different properties except from contraction velocity and concentration of enzymes, for example glycogen and myoglobin content. For general properties of type I, IIa and IIb, see table 1. The properties of type IIx is somewhere in between IIa and IIb (Sjaastad *et al.*, 2003).

The mean area of the fiber types in Standardbreds (STBs) in training are 1947 μm^2, 2457 μm^2 and 3925 μm^2 for type I, IIa and IIb respectively (Karlström *et al.*, 1991). The number of capillaries in contact with the fibers will affect how much blood that will pass the fiber and consequently also how much oxygen the muscle fiber potentially can use. The numbers of capillaries in contact with the fibers of each type relative to fiber type area differs. Fibers of type I have 2,60*10^{-3} per µm^2 while type IIa and IIb have 2,30*10^{-3} per µm^2 and 1,54*10^{-3} per µm^2 respectively. This is logical considering their use of oxygen for energy production.

Table 1. Properties of muscle fibers of type I, IIa and IIb, modified from Sjaastad *et al.,* 2003

Property	Type I	Type IIa	Type IIb
Activity of myosin ATPase	Low	High	High
Dominant method for production of ATP	Aerobic	Aerobic	Anaerobic
Content of glycolytic enzymes	Low	Intermediate	High
Number of mitochondria	Many	Many	Few
Number of capillaries	Many	Many	Few
Fiber diameter	Small	Intermediate	Large
Glycogen content	Low	Intermediate	High
Myoglobin content	High	Intermediate	Low
Typical functions	Maintain body posture	Walk, run	Jump, sprint

Inside the mitochondria energy is produced through oxidative phosphorylation. The mitochondria can replicate independently of the cell and the number of mitochondria is greater in cells with high rate of energy metabolism. A horse heart has a volume density of mitochondria of 27 % of the total cell volume while the neck has only 6 %. Mean volume density of mitochondria for the skeletal muscles is 7 % with a range of 1-14 % (Hoppeler *et al.*, 1987). The number of mitochondria in a cell reflects if the cell is creating ATP mainly aerobic or is able to rely on anaerobic metabolism for periods. In the muscle fibers of type IIb, which are recruited for fast work where oxygen cannot be delivered in sufficient amounts, the number of mitochondria is low, see table 1, and ATP can be created by glycolysis. Racehorses obtain about 30 % of their energy from anaerobic metabolism at racing speeds (Eaton *et al.*, 1995).

Oxygen consumption

To calculate the rate of oxygen consumption (VO_2) the difference in oxygen content of arterial and venous blood is multiplied by the cardiac output. At rest, VO_2 is around 3-5 ml per kg BW and minute (Eaton, 1994). As the cardiac output increases during exercise, VO_2 increases up to a plateau. At the onset of exercise, VO_2 can increase 30- or 40-fold within 60 seconds. At VO_{2max} 1 cm^3 of muscle mitochondria uses 4,75 ml oxygen per minute (Hoppeler *et al.*, 1987). VO_{2max} for an individual is determined by body size and blood volume (Kearns *et al.*, 2002). When interpreting VO_{2max} data from treadmill exercise tests the effect of the incline must be taken into consideration. An incline of 6° increases the maximal cardiac output and also the whole body oxygen delivery compared to a level treadmill (McDonough *et al.*, 2002). If exercise proceeds after VO_{2max} is reached, VO_2 and V_E will decrease (Evans & Rose, 1987), lactate will accumulate due to anaerobic metabolism and the horse will eventually become fatigued.

Genetic differences

The heart mass differs between different types of horses in absolute weight as well as percentage of BW. TBs have a heart weight of about 4-5 kg or 1 % of BW (Evans, 1994). Horses of racing type, STBs and TBs, have a greater heart weight as a percentage of BW than draft or stock type horses. Arabians have greater heart weight than draft type horses (Kline & Foreman, 1991). The total blood volume of TBs is about 9 % of BW (Evans, 1994) or approximately 50 liters of which about 30 liters is plasma (Householder & Douglas, 2005). Draft type horses have a lower total blood volume, about 6-7 % of BW (Sjaastad, *et al.*, 2003). Resting hematocrit values is 28-44 % in cold-blooded horses and 32-53 % in warm-blooded horses (Rose & Hodgson, 1994). The affinity of hemoglobin for oxygen differs between breeds (Cambier *et al.*, 2005). The weight of the spleen in relation to BW also varies between different types of horses. Racing type horses has greater spleen weight than Arabians, stock types and draft types, when horses of similar training status are compared. Draft horses have lower absolute spleen weight than the other three types (Kline & Foreman, 1991).

Ageing lowers the maximal HR that can be achieved and thereby also the performance potential. Old horses (27 years) have lower maximal HR than middle aged (15 years) and young (7 years) horses. Training can partly counteract this effect. VO_{2max} is decreased in old horses compared to middle-aged and young (Betros *et al.*, 2002). The value of VO_{2max} depends on type of horse, see table 2. For TBs and STBs VO_{2max} is normally in the range of 130-160 ml per kg BW and minute. Draft type horses (Birlenbach Potard *et al.,* 1998) and ponies (Katz *et al.,* 2005) has significantly lower VO_{2max} than the racing types, around 70 and 90 ml per kg BW and minute respectively. In an experiment where draft power of TBs and draft horses were measured there were no differences between breeds in rise in plasma lactate. This suggests that the two breeds rely on anaerobic metabolism to the same extent. When comparing horsepower per kg BW, TBs and draft horses had $10,7*10^{-3}$ and $5,44*10^{-3}$ respectively (Birlenbach Potard *et al.*, 1988).

Table 2. Maximal oxygen consumption in different types of horses

Type of horses	VO_{2max} $ml*min^{-1}*kg^{-1}$	Reference
Fit TBs	158±16	Butler *et al.*, 1991
Fit TBs	135±8	Birlenbach Potard *et al.*, 1998
Fit TBs	135±3	Eaton *et al.*, 1995
Fit TBs	152,6±4,6	Katz *et al.*, 2005
TBs before training	129,7±2,9	Evans & Rose, 1987
TBs after training	151,2±3,6	Evans & Rose, 1987
5 TBs, 1 Quarterhorse	130,5±6,6	Langsetmo & Poole, 1999
Detrained STBs	135,4±9,3	Evans & Rose, 1987
STBs	130±5,8	Hoppeler *et al.*, 1987
STBs before training	116±4,8	Hinchcliff *et al.*, 2002
STBs after training	136±5,9	Hinchcliff *et al.*, 2002
Fit draft horses	72±3	Birlenbach Potard *et al.*, 1998
Fit ponies	92±3,8	Katz *et al.*, 2005

There is a variation in stroke volume between individuals within breed. In a group of six detrained TB geldings the mean stroke volume was 2,4 ml per kg BW at VO_{2max} , ranging from 2,0 to 3,0 ml per kg BW (Evans & Rose, 1988). The relationship between capillarization, cardiocirculatory parameters and muscle characteristics in horses varies between individuals within breed. STBs have a two-fold variation within breed of capillary density, a four-fold variation in percentage type I fibers and a three-fold variation in enzyme activities (Karlström *et al.*, 1991).

Differences due to training

Whether training decreases the HR both during exercise and at rest (Pelletier *et al.*, 1987a; Pilliner & Davies, 2004) or if the resting HR remains unchanged (Evans, 1994; Kinnunen *et al.*, 2006) is not completely clear. Trained horses have higher hematocrit values than untrained horses and training can increase the affinity of hemoglobin for oxygen (Lykkeboe *et al.*, 1977). VO_{2max} is increased by training at 60 % of maximal HR (Betros *et al.*, 2002) and also by increased training up to maximal HR (Evans & Rose, 1987) and the effect remains during at least 15 weeks of inactivity (Butler *et al.*, 1991). Warm up prior to a sprint gives a higher VO_{2max} and a lower oxygen deficit than no warm up. The temperature in the skeletal muscles at the onset of the sprint is higher following a warm up (McCutcheon *et al.*, 1999) which could affect the affinity of hemoglobin for oxygen.

Differences due to management

Environmental factors and diseases can affect the capacity of the respiratory system. Management factors such as good quality forage, bedding and proper ventilation in the stable can not be emphasized enough as inhalation of airborne dust can cause respiratory ailments such as heaves which will severely impair performance in the sport horse (Art & Lekeux, 2005). There are however other things to consider when training the horse. The position of the head and neck affects upper airway flow mechanics. The flexed head-position, seen most frequently on the dressage arena, causes upper airway obstruction during strenuous exercise (Petsche *et al.*, 1995). Girth strap tensions will also have an impact on performance. A girth strap tension at rest of 10 kg or above during exhalation will shorten the distance to fatigue. A girth strap tension exceeding this value is common among racing TBs (Bowers & Slocombe, 1999).

A high sugar diet gives a higher VO_2 and a lower highest speed RER during an incremental treadmill test compared to a high starch diet. During submaximal exercise however, a high sugar diet gives a higher RER and a higher HR (Jansson *et al.*, 2002). A high fat or a high protein diet lowers RER during sub maximal exercise compared to a high starch diet (Pagan *et al.*, 1987; Pagan *et al.*, 2002). After 60 minutes of sub maximal exercise RER is lower if the horse ate hay than grain before exercise (Jose-Cunilleras *et al.*, 2002). A high fat diet can give less lactate accumulation than a low fat diet. A high fat diet containing 12 % fat of the total dietary dry matter gave lower lactate accumulation during strenuous exercise than a low fat diet containing 1,5 % fat (Sloet van Oldruitenborgh-Oosterbaan *et al.*, 2002) but a high fat diet containing approximately 5 % oil of the total dietary dry matter gave no differences compared to a high grain diet (Crandell *et al.*, 1999).

Discussion

When discussing oxygen consumption as well as physiology in general interactions between the different organs and systems in the body make it virtually impossible to pick out a few factors affecting the subject in question. Oxygen consumption has been in focus among equine scientists for a long time. Many aspects have been covered and great progress has been made. There are still, however, some question marks to straighten out. How oxygen consumption is affected by different feedstuffs is an area of great interest because of the health problems that follows diets with large amounts of grain. The results so far are somewhat contradictory as to what are the effects of substituting starch for sugar or fat.

When working with horses in a practical manner there may be three things of particular interest that affects oxygen consumption and thereby also performance of horses; genetics, training and management. The variation in oxygen consumption due to genetic factors can be in the area of 100% which makes genetics the factor that affect oxygen consumption most of the three. Variations depending on management can affect oxygen consumption to a large extent in a negative direction, such as for example poor quality stable environment, but only to a small extent in a positive direction, such as substituting starch for fat in the diet. Training generally comes somewhere in between genetics and management when it comes to affecting oxygen consumption.

Weather the horse is chosen to match a specific sport or the sport is chosen based on the capacity of a specific horse, the type of horse is the single most limiting factor as to what type of performance that can be accomplished. Breeders have selected horses of a certain type, suitable for filling their specific needs. This has not only created visual differences such as size, color and temperament but also physiological differences. While striving for development of a faster racehorse, spleen weight and heart weight have been two of the parameters breeders have unconsciously selected upon. Horses that were selected for their great endurance and stamina passed on a large number of types I and IIa muscle fibers to their progeny.

Once the horse and the discipline are chosen, appropriate training can be the difference between success and failure. In racing, oxygen consumption is one of the limiting factors and it can be positively affected by training. Training can decrease HR during exercise, and training can increase spleen weight, hematocrit and VO_{2max}. All these parameters influence the athletic capability of the horse.

A good horse with appropriate training can become a winner or a convalescent due to differences in feeding. A bad horse, however, or a good horse with poor training, can unfortunately never become a star just trough excellent feeding. Different energy sources have different effects on the horse. There is a large interest in finding a suitable substitute for grain in the ration to horses as starch can cause ailments such as glucose intolerance and gastrointestinal disturbances which in turn can cause for example laminitis and tying-up. Results from studying the possibility to use fat or sugar as energy sources for horses have been contradictory. It seems, however, that the alternatives often are comparable, or even better, than large amounts of starch. This should be of great interest to owners and trainers of racehorses.

So far most of the studies have been made on Thoroughbreds or Standardbreds because they are the most high-performing horses of today and the racing industry turn over enormous amounts of money. Several studies have shown that exercise intensity influences how different treatments affect oxygen consumption. This indicates that in order to draw parallels to other disciplines such as endurance riding, show jumping or dressage further studies have to bee conducted.

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