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DESIGN OF THE OXYGEN AND SUBSTRATE PATHWAYS

II. DEFINING THE UPPER LIMITS OF CARBOHYDRATE AND FAT OXIDATION

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Summary

This paper quantifies maximal flows of carbohydrates and lipids through the pathways supplying the mitochondria. Maximal flow rates are the main functional parameter used in testing the principle of symmorphosis, which states that structural capacities are quantitatively matched to functional demand. Only under rate-limiting conditions will all of the structural capacity be used. Dogs and goats were compared to obtain large differences in absolute rates. We exercised the animals for long enough to reach steady-state O_2 and CO_2 exchange rates at intensities eliciting 40 %, 60 % and 85 % of the maximal rate of oxygen consumption ($\dot{M}_{O_2max}$). We then calculated rates of fat and carbohydrate oxidation from the ratio of CO_2 produced to O_2 consumed (the respiratory exchange ratio). The dog's $\dot{M}_{O_2max}$ was more than twice that of the goat (6517 *versus* 3026 $\mu mol\,O_2\,kg^{-1}\,min^{-1}$). We found the same pattern of fuel selection as a function of exercise intensity in both species, and it appears to be general to mammals. Maximal rates of fat oxidation were reached at 40 % exercise intensity, where 77 % of the energy was supplied by fat. As exercise intensity increased, all additional energy was supplied by carbohydrates. We conclude that the partitioning of fuel supply to the fat and carbohydrate pathways follows the same pattern in both dogs and goats.

Key words: oxygen consumption, fat oxidation, carbohydrate oxidation, exercise, dog, goat, symmorphosis.

Introduction

In order to test for a match between structural and functional capacities in the oxygen and substrate pathways to muscle cells shown in Fig. 1 (Taylor *et al.* 1996; Weibel *et al.* 1996), it is essential to know how the fuel supply is partitioned between fats and carbohydrates as well as the maximal rates of oxidation for both. Maximal rates of oxygen consumption can be measured easily in the laboratory (see Margaria, 1976). Oxygen consumption increases with exercise intensity until an upper limit is reached. Further increases in exercise intensity occur without an increase in oxygen consumption. Instead, additional energy is supplied by anaerobic glycolysis, lactate accumulates, and the duration of the exercise is limited by metabolic acidosis. The upper limit of oxygen consumption differs between individuals. It might be $2.5\,l\,min^{-1}$ in an ordinary person and exceed $5\,l\,min^{-1}$ in an elite endurance athlete. Animals, like humans, also have well-defined maximum rates of oxygen consumption that can be measured in the laboratory (Seeherman *et al.* 1981). An elite race horse's maximal rate of oxygen consumption is 3–4 times higher than that of a cow, and a pronghorn antelope's is 3–4 times that of a goat (Weibel *et al.* 1992). These species differences provide an experimental tool, enabling us to vary fluxes through each of the steps by two- to threefold and to look for comparable differences in structural capacity. The question we address here is whether the supply of substrates shows similar differences. This we explore by studying differences in the respiratory exchange ratio, which reflects the relative contributions of fat and carbohydrates to oxidative metabolism.

The upper limit for fat oxidation is reached at low exercise intensities. Early in this century, Benedict and Cathcart (1913) discovered that the respiratory exchange ratio in humans increases with increasing exercise intensity. Low exercise intensities are fuelled primarily by fat, while high intensities, near the aerobic limit, rely mainly on carbohydrate (Bock *et al.* 1928; Brooks and Mercier, 1994; Gollnick and Saltin, 1988; Saltin and Gollnick, 1988). If we can generalize these findings to other species, we would expect that maximal rates of fat oxidation would be reached at low exercise intensities and

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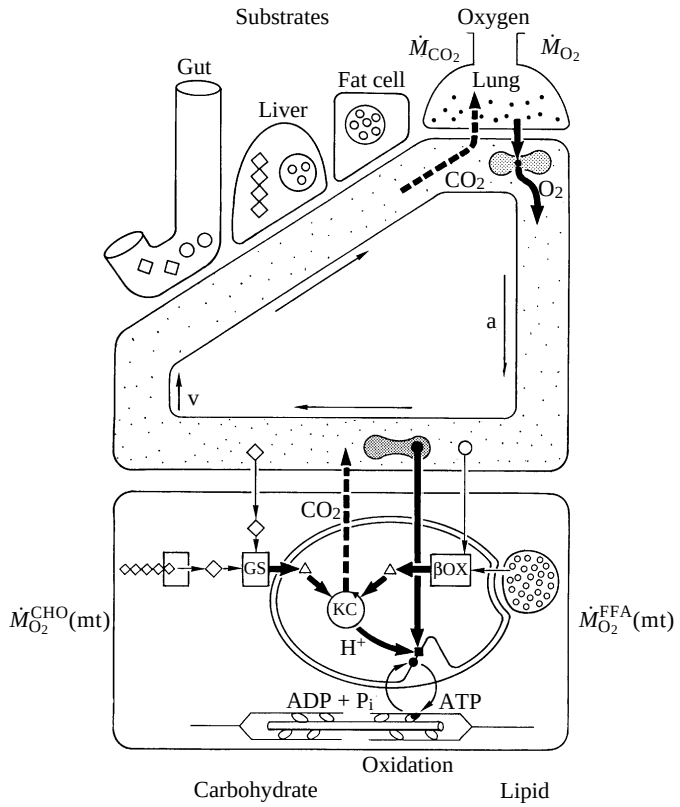

Fig. 1. Network model of the oxygen and substrate pathways from the supply organs (lung, gut, liver, fat cells) through the circulation (a, arterial; v, venous) to the muscle cells (bottom) with mitochondrion, intracellular lipid droplet, glycogen granules (row of squares) and actomyosin complex. The oxygen pathway is marked with black dots, the fatty acid pathway with circles and the glucose pathway with squares. The heavy arrows mark the transport pathways relevant for this part of the study: the O_2 supply from the lung to the mitochondrial oxidase; the flow of acetyl-CoA (triangles) to the Krebs cycle (KC) resulting from the glycolysis (GS) of glucose and β-oxidation (βOX) of fatty acids; the flow of CO_2 (broken arrows) from the Krebs cycle to the blood and its discharge through the lung; and the flow of reducing equivalents (H^+) to the terminal oxidase in the inner mitochondrial membrane (black square), where their oxidation generates the energy used to phosphorylate, at the associated F_1-ATPase, ADP to ATP. The thin arrows mark the supply of substrates from the microcirculation or from intracellular stores. The respiratory exchange ratio $\dot{M}_{CO_2}/\dot{M}_{O_2}$ depends on the relative contributions of carbohydrate $\dot{M}_{O_2}^{CHO}$(mt) and fatty acid oxidation $\dot{M}_{CO_2}^{FFA}$(mt) in the mitochondria.

maximal rates of carbohydrate oxidation at the upper limit of aerobic performance.

The fuels that are burned depend on a number of variables in addition to exercise intensity, including diet and the level of training. Rates of fat oxidation are generally increased by switching from a high-carbohydrate to a high-fat diet (Bergström *et al.* 1967; Christensen and Hansen, 1939; Jansson and Kaijser, 1982; Krogh and Lindhard, 1920). Endurance training also increases the rate of fat oxidation at the same exercise intensity in rats and humans (Brooks and Donovan, 1983; Coggan *et al.* 1990; Hermansen *et al.* 1967; Hurley *et al.* 1984, 1986; Krogh and Lindhard, 1920). The physiological basis for these changes is not clear, but the increased maximal rate of fat oxidation is accompanied by an increased concentration of enzymes for fatty acid oxidation and an increase in capillarization of the muscle (Gollnick and Saltin, 1988).

The increase in fat oxidation with training suggests that high rates of fat oxidation may be an adaptation for endurance. In humans, depletion of glycogen stores in muscle cells is an important cause of fatigue during prolonged exercise. The greater reliance on fats will spare glycogen and enhance endurance. For example, a well-trained marathon runner has higher rates of fat oxidation and larger intracellular fat stores. Fat is a much more economical store because of its approximately 10-fold higher energy density, namely $38\,kJ\,g^{-1}$ compared with $4.2\,kJ\,g^{-1}$ for hydrated glycogen.

The dog is a more specialized endurance animal than even the marathon runner. Wild canids depend on endurance hunting for their livelihood, travelling great distances in search of prey (Sheldon, 1992). Thus, we hypothesized that dogs will have adapted to the demands of endurance exercise by increasing their ability to oxidize fats at high exercise intensities. This ability should enhance their hunting success, enabling them to continue dogged pursuit of prey without depleting their glycogen stores. The pygmy goat's lifestyle provides a dramatic contrast to the dog's. It never runs for any distance, spending most of its life moving methodically from waterhole to waterhole, grazing along the way. It has no need for high rates of sustained fuel delivery. We expected that the dog's high metabolic rate would be preferentially fuelled by fat, while the sedentary goat would have relatively low rates of fat oxidation.

Materials and methods

Experimental design

We used the following strategy to determine maximum rates of fuel oxidation in dogs and goats. First, we measured maximal rates of oxygen consumption, $\dot{M}_{O_2max}$, for each animal. Then, we measured steady-state rates of carbohydrate and fat oxidation at three exercise intensities normalized to 40, 60 and 85 % $\dot{M}_{O_2max}$. The duration of exercise at each intensity was long enough to ensure that animals had achieved a steady state. Under these conditions, the respiratory exchange ratio is a reliable measure of fuel oxidation. All animals were well trained and fed a standard low-fat diet in order to minimize the effects of training and diet on fuel oxidation.

Animals, training and exercise protocols

We used four adult pygmy goats (*Capra hircus*, three females and one male, average body mass, M_b, 29.3 kg) and three adult Labrador retriever dogs (all female, average M_b 25.0 kg). All animals had unlimited access to water. Goats were fed hay and housed in a large paddock with shelter. Dogs were fed Agway Canine 2000 dog food (by mass: 25 % protein, 10 %

fat, 39 % carbohydrate, 5 % fibre, 11 % moisture and 10 % ash) and housed in an indoor–outdoor kennel. Six months prior to the beginning of the experiments, all animals had their common carotid arteries surgically relocated to a subcutaneous position in order to facilitate arterial catheterization.

Animals were run on a variable-speed inclined treadmill (goats, 18 % dogs, 29 %). Training began 3 months prior to the onset of experiments. All animals ran for 30 min or more at least four times a week. They were considered trained when their rate of oxygen consumption was reproducible at any speed from one day to the next. All measurements were made in the morning after the animals had fasted for at least 12 h. Ambient temperature was 6–14 °C.

Indirect calorimetry, $\dot{M}_{O_2max}$ and substrate oxidation

Rates of oxygen consumption, $\dot{M}_{O_2}$, and carbon dioxide production, $\dot{M}_{CO_2}$, were monitored continuously during exercise using an open-flow system (Fedak *et al.* 1981). Air was sampled from the outflow of a loose-fitting mask and O_2 and CO_2 concentrations were measured using Applied Electrochemistry analyzers (models S-3A and CD-3A, Ametek, Pittsburgh, PA, USA). Calibrations were carried out before each experiment by bleeding pure N_2 and CO_2 at known flow rates into the mask. The accuracy of the system was determined to be within ±2 %.

Maximal rates of oxygen consumption were measured as described previously (Seeherman *et al.* 1981). We used three criteria to determine when the animals had reached $\dot{M}_{O_2max}$: (1) no significant change in $\dot{M}_{O_2}$ with increasing speed; (2) reliance on anaerobic metabolism (indicated by a steady accumulation of blood lactate); and (3) a respiratory exchange ratio greater than 1.0. Blood samples were drawn from a catheter in the jugular vein and lactate concentrations were measured using a kit (Boehringer Mannheim). At the highest speed tested in each animal, blood lactate concentration exceeded 20 mmol l^{-1} after 5 min of exercise. $\dot{M}_{O_2max}$ was calculated as the mean $\dot{M}_{O_2}$ for all the runs where the rate of lactate accumulation exceeded 2 μmol ml^{-1} min^{-1}.

We determined the speeds that required oxygen consumptions equivalent to 40, 60 and 85 % of $\dot{M}_{O_2max}$ in order to measure substrate oxidation at equivalent exercise intensities in dogs and goats. Oxygen consumption was measured over a range of speeds from a slow run to $\dot{M}_{O_2max}$. The linear regression of speed on $\dot{M}_{O_2}$ allowed us to calculate the speeds that corresponded to the three exercise intensities for each animal. Rates of substrate oxidation were measured by indirect calorimetry as the animals ran for 2 h at 40 % $\dot{M}_{O_2max}$, 1 h at 60 % $\dot{M}_{O_2max}$ and 16 min at 85 % $\dot{M}_{O_2max}$. At 85 % $\dot{M}_{O_2max}$ one of the dogs did not complete the last 4 min of exercise, and at 60 % $\dot{M}_{O_2max}$ two of the dogs ran for only 50 min.

The relative proportions of fat, carbohydrate and protein oxidized during exercise will determine the ratio of CO_2 produced to O_2 consumed, or the respiratory exchange ratio (RER). Because the contribution of protein oxidation to total energy metabolism is insignificant during exercise (Bulow, 1988; Gessaman and Nagy, 1988), we assumed that the RER represented the relative proportions of fat and carbohydrate oxidation. We assumed an RER of 0.71 for pure fat oxidation, and calculated the rate of oxidation of fat and carbohydrate from $\dot{M}_{O_2}$ and RER (Frayn, 1983; McLean and Tobin, 1987):

$$\dot{M}_{O_2}^{FFA} = [\dot{M}_{O_2} \times (1 - \text{RER})]/0.29 .$$

Carbohydrate oxidation rate, $\dot{M}_{O_2}^{CHO}$, was then calculated as the difference between total $\dot{M}_{O_2}$ and $\dot{M}_{O_2}^{FFA}$. $\dot{M}_{O_2}^{CHO}$ and $\dot{M}_{O_2}^{FFA}$ represent the rates of oxidation of carbohydrate and fat, expressed as molar rates of oxygen consumption, μmol O_2 kg^{-1} min^{-1}. Because the energy produced for each mole of oxygen consumed is similar for fats and carbohydrates, these values are also approximately proportional to the energetic contribution of each substrate.

CO_2 production measured by indirect calorimetry is a reliable measure of CO_2 production by substrate oxidation only if the total blood CO_2 pool is constant during the measurements. We ensured that $\dot{M}_{CO_2}$ was not influenced by changes in the total CO_2 pool by measuring arterial and mixed venous pH and the partial pressure of CO_2 (P_{CO_2}) in each animal for the three running protocols (using a calibrated BMS3 Mk2 Radiometer blood gas analyzer). For each protocol, a steady state was reached after 2 min of exercise, and no significant change in mean pH, P_{CO_2} or total CO_2 occurred thereafter, even at the highest intensity (analysis of variance, ANOVA, P>0.3).

All results are presented as means and standard errors.

Results

Maximum aerobic capacity

As expected, the endurance-adapted dogs had an aerobic capacity ($\dot{M}_{O_2max}$) that was more than twice that of the goats (Table 1). Dogs achieved a maximum rate of oxidation of 6517±125 μmol kg^{-1} min^{-1}, while for goats it was 3026±98 μmol kg^{-1} min^{-1}. These values are similar to those reported previously for Labrador retrievers (7080 μmol kg^{-1} min^{-1}) and African goats (2376 μmol kg^{-1} min^{-1}) (Taylor *et al.* 1987; Seeherman *et al.* 1981). All of the animals were able to run for 5 min at speeds exceeding those where $\dot{M}_{O_2max}$ was reached, and the rates of lactate accumulation accounted for the additional energy required. At their fastest speeds, the rate of lactate accumulation in the blood exceeded 3 μmol ml^{-1} min^{-1} in all of the animals.

Fat oxidation

The rate of fat oxidation increased at the onset of exercise, reaching a steady level after 5–10 min at the 85 % exercise intensity and after 20–30 min at the 40 % and 60 % intensities (Fig. 2). Once a steady level had been reached, the rate of fat oxidation remained unchanged for the duration of the run. The constant rates of oxidation allowed us to calculate an average rate of fat and carbohydrate oxidation for each relative exercise intensity (Table 1). For average oxidation values, we used the

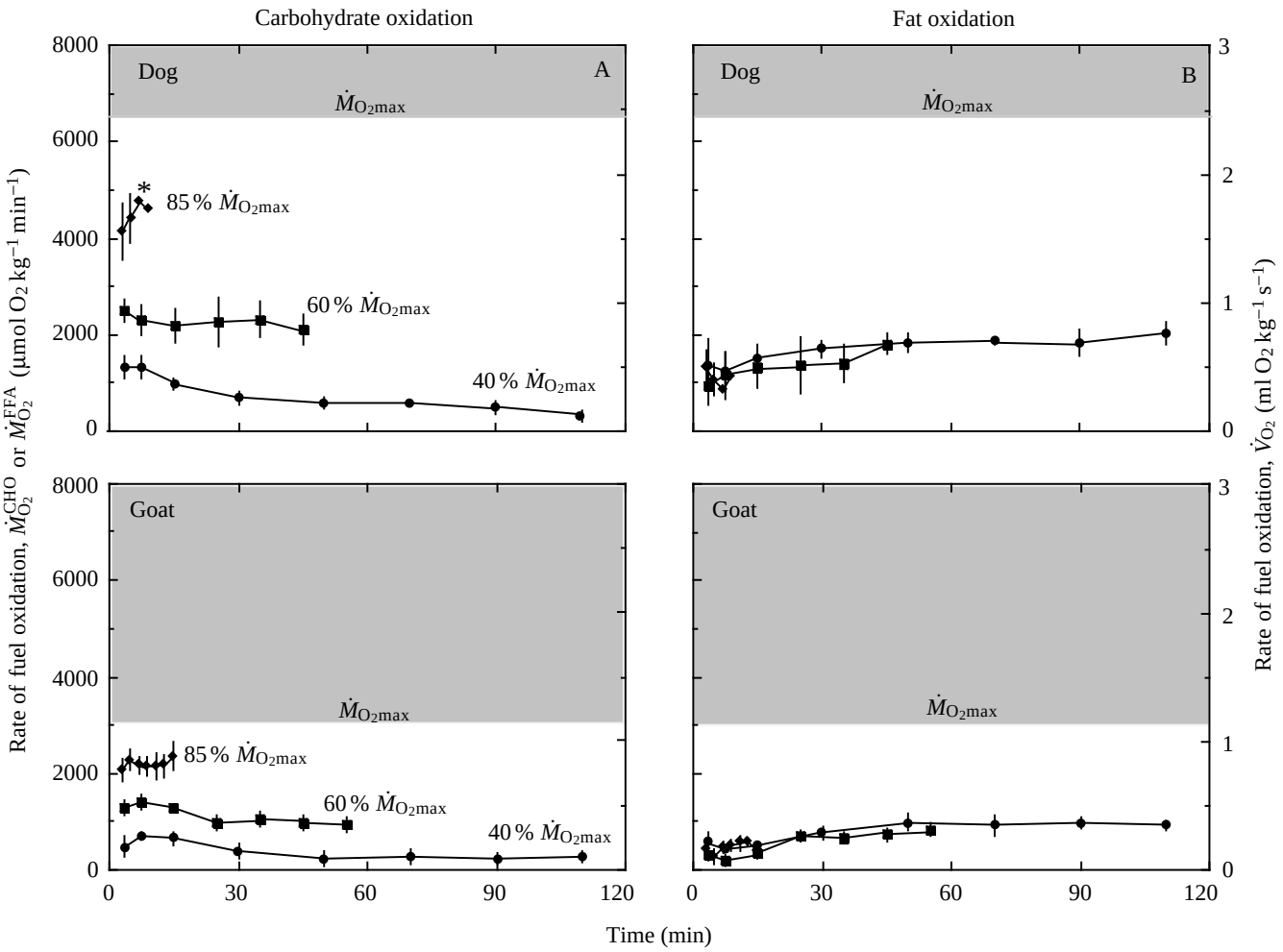

Fig. 2. Rates of carbohydrate (A) and fat oxidation (B) reached a nearly constant level in both dogs (top, *N*=3) and goats (bottom, *N*=4) after 10–20 min of exercise at intensities eliciting 40, 60 and 85 % $\dot{M}_{O_2max}$. Mean values ± one standard error are presented; * denotes *N*<3. $\dot{V}_{O_2}$ is also given.

steady levels of fat oxidation that were reached after 30 min at the 40 % and 60 % exercise intensities and after 6 min at the 85 % exercise intensity.

The steady-state rate of fat oxidation was independent of exercise intensity for the intensities we tested (Fig. 3). The maximal rate of fat oxidation is reached at 40 % $\dot{M}_{O_2max}$ in both dogs and goats. At higher exercise intensities, fat oxidation supplies about the same amount of energy. The absolute rate of fat oxidation is about twofold higher in the dog than the goat, in proportion to the difference in their aerobic capacity.

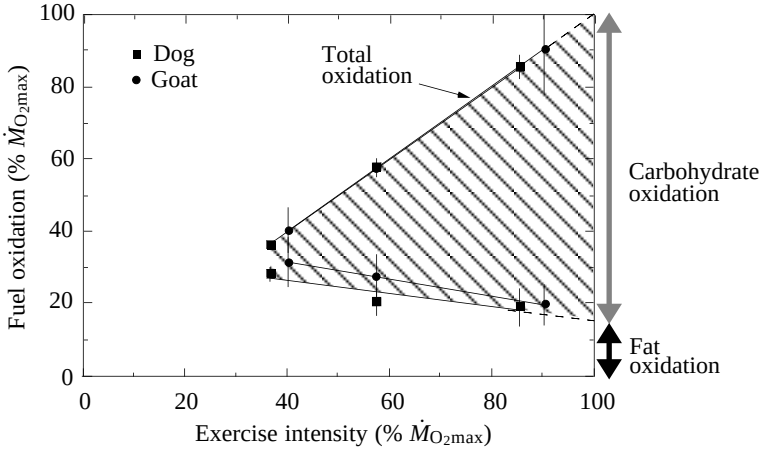

Fig. 3. Fat oxidation reached a maximal rate at 40 % $\dot{M}_{O_2max}$ in both dogs (squares, *N*=3) and goats (circles, *N*=4). The additional energy used to exercise at higher intensities came entirely from carbohydrates (hatched area). This suggests that the slower muscle fibres used at low exercise intensities are capable of using fats to supply almost all of their energy, while the faster oxidative fibres recruited at higher intensities rely almost exclusively on carbohydrates. Rates of oxidation are expressed as a percentage of $\dot{M}_{O_2max}$ and represent the mean ± one standard error.

Table 1. *Oxygen consumption, respiratory exchange ratio and rates of oxidation of fat and carbohydrate in dogs and pygmy goats at different exercise intensities*

Exercise intensity (% $\dot{M}_{O_2max}$)		Rate of oxygen consumption (μmol O_2 kg^{-1} min^{-1})	Respiratory exchange ratio	Rate of fat oxidation (μmol O_2 kg^{-1} min^{-1})	Rate of carbohydrate oxidation (μmol O_2 kg^{-1} min^{-1})
40 %	Dogs	2389±85	0.78±0.01	1847±144	541±72
	Goats	1209±52	0.78±0.03	928±145	281±134
60 %	Dogs	3759±233	0.88±0.03	1518±392	2239±382
	Goats	1729±73	0.87±0.02	745±132	985±141
85 %	Dogs	5580±312	0.93±0.02	1231±338	4348±556
	Goats	2730±222	0.94±0.01	531±129	2199±237
100 %	Dogs	6517±125			
	Goats	3026±98			

Fat oxidation reaches its maximal rate at 40 % of aerobic capacity. Carbohydrate oxidation supplies most of the additional energy at higher intensities, reaching its maximal rate at the limit of aerobic capacity (see text).

Values are means ± S.E.M.; N=3 for dogs, N=4 for goats.

Thus, the fraction of total oxidation supplied by fat is the same in both species. Fat is the predominant fuel at 40 % $\dot{M}_{O_2max}$, supplying 77 % of the fuel used at this exercise intensity (Table 1; Fig. 4). This rate of oxidation is equivalent to about 30 % of $\dot{M}_{O_2max}$ in both species (Fig. 4). At higher exercise intensities, carbohydrate supplies all of the additional energy and the relative contribution of fat decreases rapidly. At an exercise intensity of 85 % $\dot{M}_{O_2max}$, a similar absolute rate of fat oxidation provides only 19–22 % of the energy used.

Carbohydrate oxidation

Carbohydrate oxidation, like fat oxidation, reached a constant level after 5–10 min at the 85 % exercise intensity and after 20–30 min at 40 and 60 % (Fig. 2). The rate of

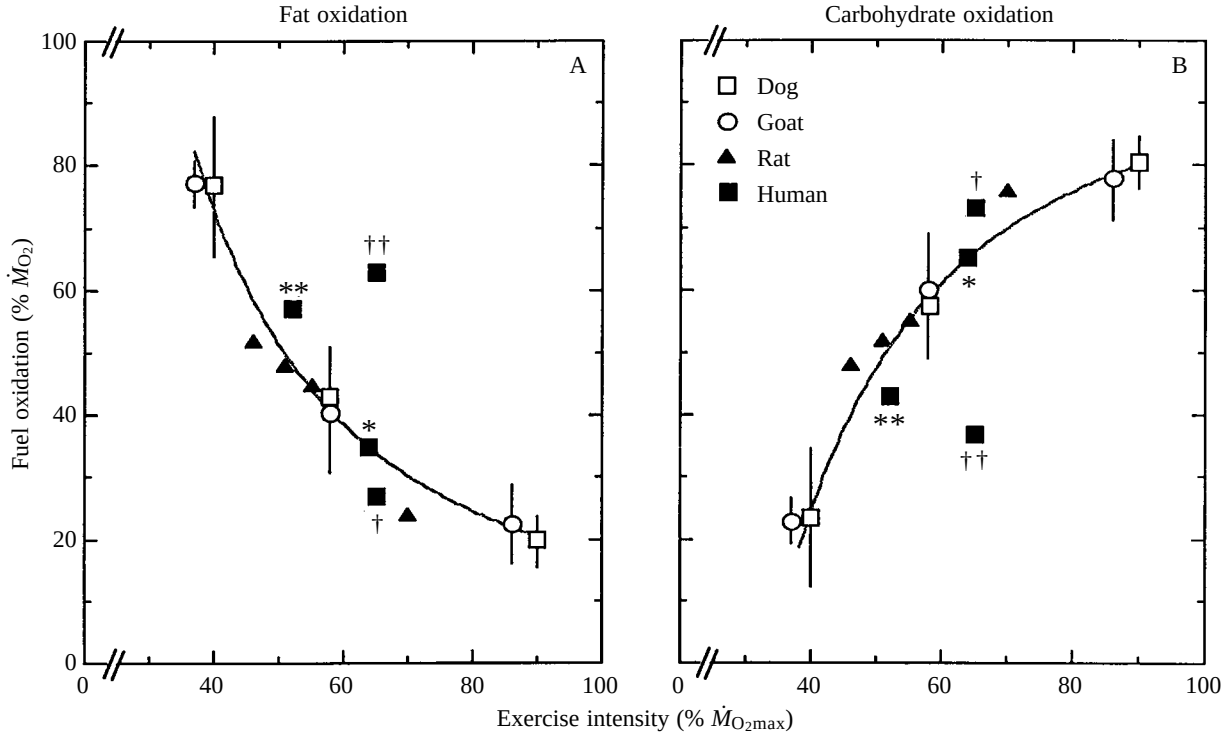

Fig. 4. The percentage of total oxidation supplied by fats (A) and carbohydrates (B) is similar at comparable exercise intensities in pygmy goats and dogs in this study, in rats (Brooks and Donovan, 1983) and in control humans fed a normal diet (* and †) (Jansson and Kaijser, 1982). The malleability of the substrate pathways is indicated by the higher rates of fat oxidation in humans after training (**) (Hurley *et al.* 1986) and after eating a very high fat diet for a prolonged period (††) (Jansson and Kaijser, 1982). Values for dogs (N=3) and goats (N=4) are means ± one standard error.

carbohydrate oxidation is highest at the beginning of exercise and falls to a steady level. We averaged the values for carbohydrate oxidation over the same time periods as for fat to obtain a single value for each exercise intensity (Table 1).

Carbohydrate oxidation supplied most of the energy at the higher exercise intensities (Fig. 3). It reached a maximum level at 85 % $\dot{M}_{O_2max}$ in our experiments. It seems likely that carbohydrate oxidation continues to increase until $\dot{M}_{O_2max}$ is reached, but we were unable to obtain steady-state values at exercise intensities above 85 %. At the lowest exercise intensity, fat was the preferred fuel in both dogs and goats and carbohydrate supplied only 23 % of total oxidation (Fig. 4). At higher exercise intensities, all of the increase in oxidation was fuelled by carbohydrates.

Discussion

Substrate oxidation: an upper limit reached

We have identified a repeatable, characteristic rate of oxidation for each fuel at any given exercise intensity. The absolute maximum rate of fat oxidation occurs at a low exercise intensity, while carbohydrate is utilized at a maximum rate when the animal exercises at its aerobic limit. Only low exercise intensities can be sustained primarily using fat. The maximum rate of fat oxidation was equivalent to approximately 30 % of $\dot{M}_{O_2max}$ in both dogs and goats. This maximum rate is reached at a low exercise intensity and does not increase with further increases in intensity.

The maximum rate of carbohydrate oxidation occurs at $\dot{M}_{O_2max}$ and could not be measured directly. The high concentrations of lactate produced at this exercise intensity make estimates of fuel use from the respiratory exchange ratio unreliable. However, by extrapolation of Fig. 3, we estimate that the maximum rate of carbohydrate oxidation reaches 80 % of the total at $\dot{M}_{O_2max}$.

It is interesting to ask whether the substrate pathway is malleable, adjusting to changes in maximal rates of oxidation that occur with changes in diet and training. In humans, a high-fat low-carbohydrate diet leads to dramatic increases in maximal rates of fat oxidation (Bergström *et al.* 1967; Christensen and Hansen, 1939; Jansson and Kaijser, 1982; Krogh and Lindhard, 1920; Phinney *et al.* 1984). After eating a high-fat low-carbohydrate diet, subjects could almost triple their maximal rate of fat oxidation (Fig. 4). The ability to oxidize fat at these rates is dependent on the duration of the diet period, increasing for as long as 4 weeks on the diet (Phinney *et al.* 1984). This adaptation is associated with a proportional increase in levels of β-oxidation enzymes (Miller *et al.* 1984; Jansson and Kaijser, 1982), suggesting increases in other steps of the fat oxidation pathway as well.

Endurance training also leads to increased rates of fat oxidation. As with the switch from a low-fat to a high-fat diet, this adaptation is also accompanied by structural changes in the fat oxidation pathways, including increases in capillary density of the muscle, mitochondrial density, intramuscular lipids, and β-oxidation and Krebs cycle enzymes (Krogh and Lindhard, 1920; Hurley *et al.* 1984, 1986; Hermansen *et al.* 1967; Hoppeler *et al.* 1973; Brooks and Donovan, 1983; Coggan *et al.* 1990). The rates of fat oxidation reported here are from trained animals, since both dogs and goats were exercised at moderate intensities for several months before the experiments began.

We had expected to find an adaptation in the dog for the preferential use of fat as a metabolic fuel, but we did not. The dog and the goat can supply approximately the same fraction of their maximum aerobic capacity from fat oxidation (20–30 %; Fig. 3). Neither species can exercise at high exercise intensities without high rates of carbohydrate oxidation. Thus, preferential use of fat is not a mechanism for conserving carbohydrate and enhancing endurance in the dog at high work rates. The sustained running speeds necessary for hunting and foraging in wild dogs may be possible because of their greater aerobic capacity rather than fuel preference. Because the dog has twice the aerobic capacity of the goat, it can run twice as fast while operating at the same relative exercise intensity. Thus, the speed at which fat oxidation can supply almost all of the energy (i.e. speeds below 40 % $\dot{M}_{O_2max}$) is twice as high in the dog.

Field observations of wild canids and goats support the idea that a greater aerobic capacity may allow an animal to travel faster and forage more widely while fuelling muscles by fat oxidation. Wolves commonly trot at approximately 2.25 m s^{-1} (5 miles per hour) when hunting over long distances (Mech, 1981). This speed requires an energy consumption of approximately 1700 μmol O_2 kg^{-1} min^{-1} (Taylor *et al.* 1982). If the $\dot{M}_{O_2max}$ of wolves is equal to or greater than that of the dogs used in this study, this rate of oxidation is equivalent to an exercise intensity of 25 % $\dot{M}_{O_2max}$ or less. This is within the range of exercise intensities that can be fuelled primarily by fat; thus, wolves can travel for great distances at this speed with little carbohydrate depletion. Goats have a similar running economy but a lower $\dot{M}_{O_2max}$, so the same running speed would require an energy consumption equivalent to 65 % $\dot{M}_{O_2max}$ in the goat. At this exercise intensity, more than half of the energy would be supplied from carbohydrate oxidation. Goats rarely run, but forage at a slow walking speed and low exercise intensities (Hudson and White, 1985). Thus, the high aerobic capacity of canids may be essential to maintain the greater rates of fat oxidation necessary for a hunting lifestyle.

After the first 10–20 min of exercise, the maximum rate of fat oxidation was independent of the exercise duration in our experiments. Some investigators also report nearly constant rates of fat oxidation for prolonged periods after an initial increase (Bergström *et al.* 1967; Davis *et al.* 1990; Hedman, 1957; Hermansen *et al.* 1967; Krogh and Lindhard, 1920). Others, however, find that rates of fat oxidation continue to increase during one to several hours of exercise (Christensen and Hansen, 1939; Bergström *et al.* 1967; Hurley *et al.* 1986; Coggan *et al.* 1990; Edwards *et al.* 1934). An explanation for this discrepancy may be related to differences in exercise intensity in the different experiments. The rate of fat oxidation appears to be constant at exercise intensities close to or

exceeding those that elicited maximal rates of fat oxidation in our experiments (i.e. >40 % $\dot{M}_{O_2max}$). In contrast, in experiments where a continual increase is seen for hours, the exercise intensity is low and the absolute rate of fat oxidation remains low throughout the experiment, even after the increases were recorded. It seems likely that these investigators would have found constant rates at higher exercise intensities where maximal rates of fat oxidation had been reached.

Strategies for fuel supply: common solutions

Contrary to our expectations, we did not find a relatively higher rate of fat oxidation in the endurance-adapted dog. The maximum rate of fat oxidation varied in direct proportion to the maximal aerobic limit in the dog and the goat. Both species could supply fat for oxidation at 30 % of their $\dot{M}_{O_2max}$. The dog has the advantage of a higher $\dot{M}_{O_2max}$, allowing it to burn fat at higher absolute rates. This observation led us to ask whether the maximal rate of fat oxidation is the same fraction of maximal oxidation rates in mammals generally. It seemed possible that this direct proportionality might be a common pattern among mammals, particularly since we observe it in such dissimilar animals in terms of both endurance and digestive systems as the dog and the goat. We therefore plotted steady-state values from the literature for humans and rats together with our data from dogs and goats (Fig. 4). The resulting figure demonstrates that these species utilize the same fuel mixture at any given fraction of their maximum aerobic capacity. The outliers represent humans eating high-fat diets. Their rates of fat oxidation are twice those of individuals eating low-fat diets. It would seem, then, that there may be adaptive capacity for adjusting to diet.

What determines fuel preference?

Why is the maximum level of fat oxidation the same fraction of $\dot{M}_{O_2max}$ in species with very different aerobic capacities? The relative contribution of each fuel at a given exercise intensity may reflect differences in the muscle fibres that are recruited and the fuel preference of individual fibres. Slow, very oxidative muscles (Type I) are recruited when animals run slowly. As speed is increased, these slow oxidative fibres remain active while additional faster fibres (Type II) are recruited (Armstrong, 1988). This pattern directly parallels the pattern of fuel use: slow running is fuelled primarily by fat, and as speed increases all additional oxidation is fuelled by carbohydrate. This suggests that the different muscle fibre types are specialists for different fuels.

Conclusions

Dogs and goats show similar patterns of metabolic substrate use across a range of exercise intensities. Dogs have a 2.2-fold greater aerobic capacity than goats; this is achieved by higher rates of oxidation of both fat and carbohydrate. A quantitative comparison of fuel use in dogs and goats indicates the following.

(1) There are clearly defined maximal rates of fat and carbohydrate oxidation in dogs and goats.

(2) Maximum rates of fat oxidation occur at about 40 % $\dot{M}_{O_2max}$ in both dogs and goats. At low exercise intensities, most of the energy is supplied by fat oxidation (approximately 80 % at an exercise intensity of 40 % $\dot{M}_{O_2max}$). As exercise intensity increases, carbohydrate oxidation supplies the additional energy, reaching its maximal oxidation rate at the limit of aerobic capacity.

(3) The observed pattern of recruitment of fuels with relative exercise intensity appears to represent a general mammalian pattern and may be related to the order of recruitment of fibres specialized for oxidizing different fuels.

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