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Potard, U. Silke Birlenbach, David E. Leith, and M. Roger Fedde. Force, speed, and oxygen consumption in Thoroughbred and draft horses. *J. Appl. Physiol.* 84(6): 2052–2059, 1998.—Thoroughbred (TB) and draft horses (DH) have long been selected for tasks of very different intensities and force-speed relationships. To study their adaptations, we measured O_2 consumption and related variables in three TB and four DH during progressive exercise tests on a level treadmill. The horses exerted a draft force of 0, 5, 10, 15, or 20% of their body weight at speeds that increased by 2 m/s every 3 min until they could not maintain that speed. We found that TB could exert the same draft forces as DH and, at each force, TB achieved about twice the speed, twice the external power, and twice the O_2 consumption as DH; thus the two breeds had the same gross efficiencies. We also found maximal O_2 consumption of TB to be about twice that of DH (134 vs. 72 ml·kg^{-1}·min^{-1}, respectively), suggesting adaptations to high-intensity exercise. Peak efficiency was reached at lower speeds in DH than in TB, suggesting adaptations to high-force, low-speed exercise. These differences between TB and DH in force-speed and aerobic capacities and in speed for peak efficiency likely reflect different contraction velocities in locomotor muscles.

equine; exercise; force-speed relationships; external power; gross efficiency

SELECTIVE BREEDING of animals can elicit highly specialized characteristics. This practice provides an opportunity to study adaptive capacities, including the nature, rate, and extent of the structural and physiological changes that can be achieved. We thought that comparison within a species of breeds selected for different kinds of exercise might be a useful approach to study their adaptations.

Thoroughbred (TB) and draft horses (DH) have long been bred for different tasks. TB have been selected for bursts of near-maximal exercise at high speed with low external forces, whereas DH have been selected for long-sustained submaximal exercise at low speeds against high external forces. These tasks differ in two basic ways: they involve very different exercise intensities, and they lie near opposite ends of what can be thought of as external force-speed curves analogous to muscle force-velocity curves (14).

To the extent that TB and DH have adapted to these different activities, we can expect differences in their structure and function; that is, they can serve as an "allometric pair" within a single species. Regarding the musculoskeletal system, we know that TB can run faster than DH, and we expected DH to be able to exert greater draft forces (expressed as a fraction of body weight). We also suspected that maximal power and gross efficiency, as well as the force-speed combinations

at which they are reached, might differ between these breeds. We expected TB to have greater aerobic capacity than DH, with associated differences in their gas exchange and transport systems.

To test these expectations, we measured O_2 consumption ($\dot{V}O_2$) and related variables and calculated external power and gross efficiency in TB and DH during progressive treadmill exercise in a series of experiments covering the widest feasible matrix of speed and draft force. We also measured maximal O_2 consumption ($\dot{V}O_{2\,max}$) of the two breeds, the first such measurements in DH as far as we know. The experimental protocol and procedures were approved by the Animal Care and Use Committee of Kansas State University.

METHODS

Animals. We studied four healthy DH geldings (ranging in age from 4 to 13 yr; two Percherons, averaging 805 ± 16 kg body wt; and two Belgians, averaging 750 ± 7 kg in body wt) and three TB (ranging in age from 6 to 7 yr and averaging 553 ± 19 kg in body wt). (Note: we refer to Belgians and Percherons as a single "breed," i.e., DH). The Belgians were allowed to canter, but, at the owner's request, the Percherons were not. The horses were kept in good nutritional status on suitable pasture or in pens with shelters and were weighed weekly; they gained an average of 16 kg during the course of the experiment. They were given routine hoof and medical care. For conditioning and learning of the new tasks required for the study, TB worked in harness and DH exercised on the treadmill twice weekly for 5 mo. Then, for 3 mo before the experiments, both groups practiced the planned experimental protocols at least twice weekly on the treadmill, covering the full range of force and speed combinations. During this time, preliminary measurements were made to determine appropriate bias flow rates through the $\dot{V}O_2$-measurement system (Fig. 1). This period also served to further habituate the horses to the experimental tasks and conditions and to establish similar states of fitness in the two groups. To maintain this state, all horses were exercised at least weekly throughout the remainder of the study, either in experiments or in training sessions.

Exercise system. The horses exercised on a level treadmill (SATO, Uppsala, Sweden) in an air-conditioned laboratory equipped with cooling fans; they wore a safety harness attached to an overhead treadmill cutoff switch. They also wore suitable collars and harness attached to a cable running over pulleys to support a basket that was free to move vertically in a steel frame behind the treadmill (Fig. 1). By keeping the basket (and any added weight) suspended, horses could exert a known constant draft force while running at selected speeds. Horses lifted the basket by moving forward on the treadmill; an exercise bout ended when, despite urging, they no longer maintained that forward position.

Protocol. The experiments covered the widest feasible matrix of force and speed. For an experimental run, a draft force was selected equivalent to 0, 5, 10, 15, or 20% of the
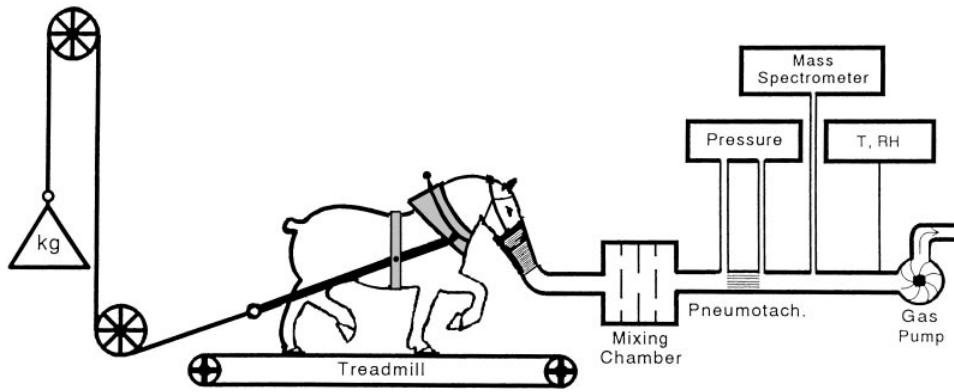
Fig. 1. Experimental arrangement. While exercising on a level treadmill at incremental speeds, horses exerted a draft force, scaled as a percentage of their body weight, by lifting a vertically movable weight basket that was connected to horse via a pulley and harness system. Pumps at outlet of gas-collection system created a gas flow through an open face mask, mixing chamber, and pneumotachometer. Pressure difference across pneumotachometer (pneumotach.), concentrations of O_2 and CO_2 in gas, and gas temperature (T) and relative humidity (RH) were measured.

animal's body weight. Two sets of measurements were then made with the horse standing quietly on the treadmill: first, the horse exerted no force, and then, having moved to the front of the treadmill, it maintained the selected force for 3 min. The horse then exerted the selected force at speeds that increased by 2 m/s every 3 min until it no longer maintained position on the treadmill. Thus each individual's peak speed at a given force was determined as the highest speed sustained for 3 min at that force. To obtain measurements during steady-state conditions of gas exchange, we collected data during the third minute at each speed (20). Postexercise measurements were taken 1, 3, 5, and 10 min after the treadmill was stopped and the weights were released.

Gas exchange measurements. $\dot{V}O_2$ and CO_2 production ($\dot{V}CO_2$) were measured with an open-flow system (Fig. 1). Pumps drew a bias flow of room air through the loosely fitting face mask and thence through the system, at flow rates that varied with exercise intensity (5–167 l/s for TB, 6–123 l/s for DH) and were selected as follows. In preliminary experiments, we measured $\dot{V}O_2$ of some horses in the experimental protocol, estimated total ventilation (assuming a ventilatory equivalent for O_2 of 25) (15), and then estimated peak expiratory flow rates, assuming sinusoidal flow. Bias flows were set at about twice the estimated peak flow to ensure complete collection of expired gas, which was verified by the absence of CO_2 in gas continuously sampled anywhere at the inlet of the face mask with a respiratory mass spectrometer (model 1100, Perkin-Elmer, Pomona, CA). Expired gas thus collected was led via conduits (15 cm diameter, totaling 7.5 m in length) through a baffled mixing chamber consisting of one 200-liter chamber for measurements in standing animals or six such chambers connected in parallel for measurements during exercise. Adequate gas mixing was observed at all speeds, as judged by the absence of fluctuations in the composition of mixed expired gas (O_2 and CO_2 fractions). The compositions of room air and mixed expired gas were measured with the respiratory mass spectrometer, which was calibrated before and after each experiment with gases of known composition provided by precision gas-mixing pumps (model 301a-F, Woesthoff, Bochum, Germany). Temperature and relative humidity of the mixed expired gas were determined with a digital thermohygrometer (model 880 with model 882 sensor, General Eastern Instruments, Watertown, MA) inserted in the system near the gas-sampling site. Total gas flow was calculated from the pressure drop across Fleisch-type pneumotachometers ("flow-straightener" elements, Meriam Instruments, Cleveland, OH; 15 cm diameter for preexercise and 25 cm diameter for exercise measurements), measured with a suitable differential pressure transducer (model MP-45, Validyne, Northridge, CA). The pressure transducer was calibrated before and after each experiment with a

precision water manometer (model A7A micromanometer, Meriam Instruments). The flow-measuring system was calibrated by using a nitrogen dilution technique (10).

Plasma La⁻. Blood samples were taken during the last minute of exercise at each speed from a catheter placed in the pulmonary artery, and they were stored on ice in tubes containing EDTA. Within 10 min after each experiment, the plasma was removed and frozen. Plasma La⁻ concentration, [La⁻], was measured within 14 days by using an automated lactate analyzer (model 23L, Yellow Springs Instruments, Yellow Springs, OH).

Stride frequency. Stride frequency was measured from a record of footfall-related treadmill vibrations sensed by a pressure transducer (P23Db, Gould, Cleveland, OH) clamped to the treadmill frame. Footfall and gait also were noted manually.

Data recording and processing. Footfall signals were amplified (model 8811A, Hewlett-Packard, Waltham, MA) and recorded on a multichannel pen recorder (model 481, Gould). Data obtained from the mass spectrometer and pressure signals from the pneumotachometer were recorded and processed on-line with a computer (MTech, Microtech, Lawrence, KS) and a commercial software package (CODAS 5.51, DATAQ, Akron, OH).

Calculations. Stride length was determined as the ratio of treadmill speed to stride frequency. $\dot{V}O_2$ and $\dot{V}CO_2$ (STPD) were calculated from inspired and mixed expired O_2 and CO_2 fractions and total gas flow, after appropriate corrections for temperature, barometric pressure, and water vapor pressure (26, 27), and divided by body weight to obtain the mass-specific values used here. Respiratory exchange ratio was calculated as the $\dot{V}CO_2$-to-$\dot{V}O_2$ ratio. Mass-specific external power ($\dot{W}$) was calculated as (force·speed)/body weight. Gross efficiency was then derived as the $\dot{W}$-to-$\dot{V}O_2$ ratio by using appropriate transformations and a caloric equivalent for O_2 of 5.0397 kcal/l. Because [La⁻] increases linearly as a function of time during constant high-intensity exercise (after a delay of up to 30 s) (2, 21), La⁻ accumulation rate (d[La⁻]/dt) was calculated as the difference in [La⁻] between two speeds divided by the time interval (33).

$\dot{V}O_{2max}$. $\dot{V}O_{2max}$ was determined in separate experiments. After a 3-min warm-up at 3 m/s, horses exerted a force equal to 10% of their body weight in a series of exercise bouts lasting 3 min or less at each of the following speeds: 4, 5, 5.5, or 6 m/s for DH and 8, 9, 10, or 11 m/s for TB. At this draft force, DH could not complete 3 min at 5.5 and 6 m/s and TB could not complete 3 min at 10 and 11 m/s. To see if steady-state conditions of gas exchange were reached, $\dot{V}O_2$ was measured at 30, 75, 120, and 165 s during each exercise bout. [La⁻] was measured in jugular venous blood sampled from a 14-gauge intravenous catheter (Delmed A-cath, Du-

pond, Canton, MA) before exercise, just before cessation of exercise at the designated speed, and at timed intervals after the exercise ceased.

Statistical analyses. A repeated-measures analysis of variance was performed by using commercial software (SAS, SAS Institute, Cary, NC), partitioning between breeds, horses within breeds, force, and the interaction between breed and force. Two-tailed tests of a multiple-comparison method (general linear model and procedure of least square means) were also used to compare results.

Two within-breed comparisons were made. *1*) At a given force, $d[La^-]/dt$ as a function of speed was compared to see whether a significant rise occurred; and *2*) between forces, peak $\dot{V}O_2$ ($\dot{V}O_{2peak}$), $[La^-]$, $d[La^-]/dt$, $\dot{W}$, gross efficiency, and regression lines of stride frequency and $\dot{V}O_2$ as functions of speed were compared to see whether they varied with force. Two between-breed comparisons also were made. *1*) At a given force, peak $\dot{W}$, gross efficiency, $[La^-]$, $d[La^-]/dt$, and regression lines of stride frequency and $\dot{V}O_2$ as functions of speed were compared to see whether they varied with breed; and *2*) preexercise $\dot{V}O_2$ and $\dot{V}O_{2peak}$, averaged for all force-speed relationships, were compared to see whether they differed between breeds. Means that differed with a $P \le 0.05$ were considered to be significantly different.

For analysis of $\dot{V}O_{2max}$, we used the highest $\dot{V}O_2$ observed and the $[La^-]$ obtained just before cessation of exercise at each speed. The highest $\dot{V}O_2$ values at each speed were averaged for all horses within a breed; differences among speeds were tested with Fisher's least significant difference test (SAS); means differing with $P \le 0.05$ were considered significantly different.

RESULTS

$\dot{V}O_2$. At each force, $\dot{V}O_2$ increased linearly with speed (Fig. 2), the slope of the relationship being greater for higher forces. The rate of change of $\dot{V}O_2$ with speed at the various draft forces did not differ between TB and DH, except at a force of 15% of body weight. TB reached the same $\dot{V}O_{2peak}$ regardless of the force-speed combination used, and DH nearly did so (Table 1). $\dot{V}O_{2peak}$ for TB was twice that of DH (Fig. 3), with the average $\dot{V}O_{2peak}$ over all draft forces being 117 ± 3 and 59 ± 4 ml·min^{-1}·kg^{-1}, respectively.

$\dot{V}O_{2max}$ of TB was about twice that of DH (135 ± 8 ml·min^{-1}·kg^{-1} at 10 m/s vs. 72 ± 3 ml·min^{-1}·kg^{-1} at 5.5 m/s, respectively; Fig. 4, Table 2). Acceptable plateaus of $\dot{V}O_2$ were found at 5–5.5 m/s in DH and at 9–10 m/s in TB (Fig. 4), except for one animal. Horses could maintain the highest of our test speeds for only 45–120 s. Peak $d[La^-]/dt$ and respiratory exchange ratios were high in both TB and DH (Table 2). Heart rates were also high (Table 2), reaching the plateau values reported by Birks et al. (2) in horses exercising at $\dot{V}O_{2max}$. By these criteria and the observed plateaus of $\dot{V}O_2$, we believe the horses had achieved $\dot{V}O_{2max}$.

La^-. At any given force, TB reached a higher speed than DH before $[La^-]$ began to rise. With increasing force, the rise in $[La^-]$ began at lower speeds in both breeds (Fig. 2). TB reached the same peak $d[La^-]/dt$ regardless of the force-speed combination used, and DH nearly did so (Table 1). At the peak speed, neither $d[La^-]/dt$ (except at a draft force equal to 20% of body wt) nor $[La^-]$ differed between TB and DH at any force (Table 1).

Force, speed, and power. Draft forces ranged up to 20% of the animals' body weight for both TB and DH. As speed increased, maximum sustainable force decreased (connected data points in Fig. 5). At each force, including 0% body weight, TB reached peak speeds about twice those of DH; thus the force-speed curves converge as force increases, and the force intercepts may not differ.

Maximal $\dot{W}$ ($\dot{W}_{max}$) of TB was about twice that of DH, 7.9 vs. 4 W/kg (or 10.7 and $5.44 \cdot 10^{-3}$ horsepower·kg^{-1}), respectively (isopleths in Fig. 5). $\dot{W}_{max}$ was achieved at several force-speed combinations (plateaus in Fig. 6). At $\dot{W}_{max}$, force was 10–20% of body weight in both breeds, with TB achieving twice the $\dot{W}_{max}$ at twice the speed of DH. Data from Procter et al. (28) suggest that at very low speeds and high forces, $\dot{W}_{max}$ of DH diminishes (Fig. 6); indeed, for both breeds $\dot{W}$ must approach zero as speed approaches zero.

Gross efficiency. The differences in external power achieved by TB and DH were matched by differences in $\dot{V}O_2$, so both breeds reached maximal gross efficiencies of ~20% (Fig. 7). For TB, external power and gross efficiency both plateaued over the same range of force-speed combinations (Figs. 6 and 7). For DH, we found no plateau of gross efficiency; instead, it reached a maximum at the lowest speed our treadmill permitted, in good agreement with data from Procter et al. (28) (Fig. 7).

Stride length, stride frequency, and gait. Our protocol did not establish the exact speeds at which gait changes occurred. The walk-trot transition was ~2 m/s in both breeds. The transition from trot to canter (gallop) was between 4 and 6 m/s for TB and between 6 and 8 m/s in DH, compared with allometric predictions of 5.9 and 6.4 m/s for TB and DH, respectively (13). Changing draft force did not cause a change in gait at any speed.

Stride patterns varied with speed in known ways (6) that did not differ between breeds: both TB and DH tended to increase speed by increasing stride length more than stride frequency (Fig. 8). Stride frequency appeared to be greater in TB than in DH during the canter (for example, mean stride frequency of 1.84 and 1.68 Hz, respectively, at 8 m/s with no draft force). At a given speed, increasing force was associated with increased stride frequency and decreased stride length, as observed by others (19). At 2–6 m/s, slopes of stride frequency as a function of speed differed between breeds only at a draft force equal to 10% of body weight. Thus the locomotor (stride) patterns for increasing speed at no draft force and when changing force at constant speed were similar in TB and DH.

DISCUSSION

We first discuss major findings under three headings: aerobic capacities, force-speed relationships, and power and efficiency.

Aerobic capacities. Mean $\dot{V}O_{2max}$ of 134 ml·kg^{-1}·min^{-1} in our TB can be compared with reported values ranging from 129 and 163 ml·kg^{-1}·min^{-1} for detrained and conditioned TB, respectively, to an extreme of 198 ml·kg^{-1}·min^{-1} (7–9, 16). Mean $\dot{V}O_{2max}$ for our DH was

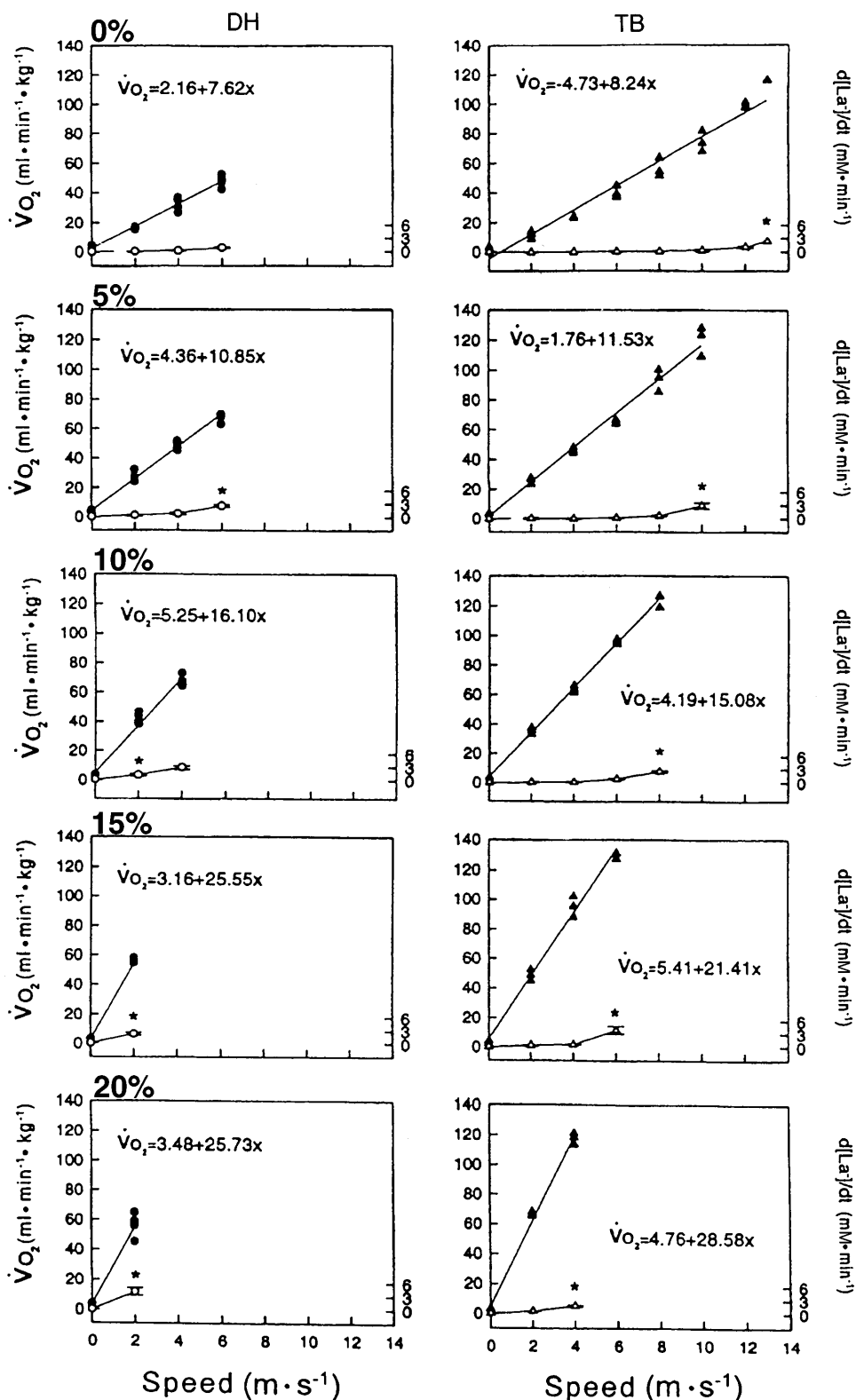Fig. 2. Effect of increasing speed and draft force (0–20% of body weight) on mass-specific O_2 consumption ($\dot{V}O_2$) and plasma La^- accumulation rate ($d[La^-]/dt$) in Thoroughbred (TB) and draft horses (DH). Solid symbols, values of $\dot{V}O_2$ (*left y*-axis) vs. speed for individual horses; regression equation is shown for each force. Open symbols, means ± SE of $d[La^-]/dt$ (*right y*-axis) vs. speed. Slopes of $\dot{V}O_2$ vs. speed within breeds were significantly different with increasing force, except for DH at forces of 15 and 20% body weight. At a given force, slopes of $\dot{V}O_2$ vs. speed were not significantly different between breeds except at a force of 15% of their body weight. *Means significantly different from preceding speed, $P \le 0.05$.

72 ml·min⁻¹·kg⁻¹. We believe these are the first measurements of $\dot{V}O_{2\,max}$ in DH. Procter et al. (28) reported $\dot{V}O_2$ up to 43 ml·min⁻¹·kg⁻¹ in one DH. Using Nadaljak's (25) data, we estimate that his horses may have reached a $\dot{V}O_2$ of ~84 ml·kg⁻¹·min⁻¹ during near-maximal draft work (speed = 1.6 m/s, force = 32% body wt); however, his group of horses included non-draft-type animals.

Thus we found, as expected, that TB are capable of greater mass-specific $\dot{V}O_2$ than are DH. We think the

Table 1. *Energetic, mechanical, and locomotor variables for Thoroughbred and draft horses before exercise and at peak force-speed combinations*

Force, %BW	Speed, m/s	Peak $\dot{V}_{O_2}$, ml·min^{-1}·kg^{-1}	[La$^-$], mM	d[La$^-$]/dt, mM/min	Power, W/kg	Gross Efficiency, %	SF, Hz	SL, m
			Thoroughbred horses (n = 3)					
Preexercise		4.9 ± 0.3[a]	0.8 ± 0.0					
Exercise								
0	12.3	105.2 ± 5.5[b]	7.3 ± 1.7[b,g]	1.5 ± 0.5[b]	0.0 ± 0.0	0.0 ± 0.0	2.11 ± 0.05	5.83 ± 0.03
5	10.0	120.6 ± 5.7[b]	12.4 ± 1.9[b,g]	3.0 ± 0.7[b]	4.9 ± 0.0	11.6 ± 0.5	1.87 ± 0.02	5.34 ± 0.06
10	8.0	124.0 ± 2.5[b]	11.4 ± 1.0[b,g]	2.6 ± 0.2[b]	7.9 ± 0.0	18.0 ± 0.4	1.87 ± 0.07	4.30 ± 0.15
15	5.3	118.0 ± 11.4[b]	10.5 ± 4.5[b,g]	2.7 ± 1.3[b]	7.9 ± 1.0	18.8 ± 0.6	1.68 ± 0.06	3.15 ± 0.29
20	4.0	117.7 ± 2.1[b]	6.7 ± 0.5[b,g]	1.7 ± 0.2[b,h]	7.9 ± 0.0[i]	19.0 ± 0.3[g]	1.50 ± 0.05	2.67 ± 0.09
			Draft horses (n = 4)					
Preexercise		3.4 ± 0.1[a]	0.8 ± 0.0					
Exercise								
0	5.9	47.9 ± 2.0[e]	4.4 ± 0.7[b,g]	0.9 ± 0.2[c]	0.0 ± 0.0	0.0 ± 0.0	1.59 ± 0.04	3.69 ± 0.12
5	5.9	67.4 ± 1.5[f]	12.0 ± 1.2[b,g]	2.6 ± 0.3[c]	2.9 ± 0.1	12.2 ± 0.5	1.64 ± 0.05	3.59 ± 0.15
10	4.0	67.6 ± 1.9[f]	12.6 ± 1.9[b,g]	2.8 ± 0.4[c,d]	4.0 ± 0.0	16.6 ± 0.4	1.42 ± 0.03	2.82 ± 0.07
15	2.0	56.5 ± 0.7[e,f]	7.3 ± 1.1[b,g]	2.1 ± 0.4[c]	3.0 ± 0.1	15.3 ± 0.4	1.15 ± 0.03	1.79 ± 0.06
20	2.0	56.2 ± 4.1[e]	12.7 ± 2.7[b,g]	3.9 ± 0.8[d,h]	4.0 ± 0.1[i]	20.7 ± 1.5[g]	1.12 ± 0.06	1.84 ± 0.07

Values are means ± SE of data obtained preexercise and at highest speed completed by each horse at a given force. BW, body weight; $\dot{V}_{O_2}$, O_2 consumption; [La$^-$], plasma La$^-$ concentration; d[La$^-$]/dt, rate of plasma La$^-$ accumulation; power, mass-specific external power; SF, stride frequency; SL, stride length. [a]No significant difference between breeds. Within-breed comparisons: [b]no significant difference with increasing draft force; [c]no significant differences among forces of 0, 5, 10, and 15% BW; [d]no significant difference between forces of 10 and 20% BW; [e]no significant differences among forces of 0, 15, and 20% BW; [f]no significant differences among forces of 5, 10, and 15% BW. Between-breed comparisons: [g]no significant difference at any maximal force-speed combination; [h]significant difference at 20% BW; [i]significant difference of peak values at 20% BW. $P \leq 0.05$.

twofold difference reflects adaptation of TB to higher exercise intensities, presumably influenced by task-specific selective breeding and genetic differences rather than conditioning. Our TB and DH were conditioned similarly, and, furthermore, training increases $\dot{V}_{O_2 max}$ of TB by a factor of only ~1.2–1.3 (7).

Genetic differences underlying the different aerobic capacities of TB and DH might exist in their gas exchange and transport systems (not addressed in this report) and in their O_2 sinks, i.e., muscles, which account for most of the $\dot{V}_{O_2}$ during heavy exercise (38). Muscle differences of several kinds may help explain the greater mass-specific aerobic capacity of TB. Muscle constitutes 53% of the body weight in adult TB but only 44% in DH foals and, perhaps, in adult DH (12). Also, during peak exercise in our tests, TB and DH may have used their muscles differently; for example, TB may have recruited a greater fraction of their muscle mass. We think it likely that intrinsic muscle properties

(force-velocity characteristics) also differ between the two breeds and underlie their differing aerobic capacities. That is, locomotor muscles of TB may achieve higher contraction velocities at similar forces, which are associated with higher rates of ATP hydrolysis and higher $\dot{V}_{O_2}$. We would expect associated differences in muscle mitochondrial densities.

We found no differences in these experiments between breeds in the peak rates or extents of rise in plasma [La$^-$], suggesting similar dependence on anaerobic metabolism. However, our study was not designed to see whether TB and DH had different capacities or tolerances for anaerobic metabolism, and we do not know whether DH ever reach the extraordinarily high [La$^-$] (35 mmol/l) reported for TB during maximal exercise (34).

Aerobic capacities of both breeds exceeded those predicted by allometric equations for mammals their size (37); that of TB is 3.1 times and that of DH 1.8
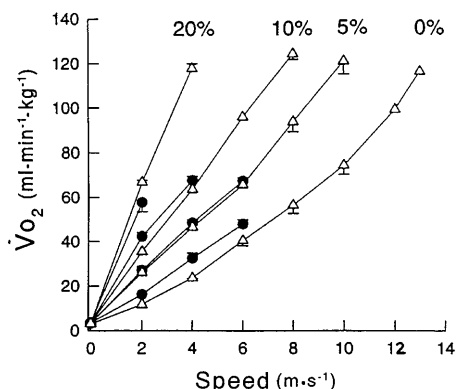

Fig. 3. Mean (±SE) $\dot{V}_{O_2}$ for TB (△) and DH (●) as a function of speed and draft force.
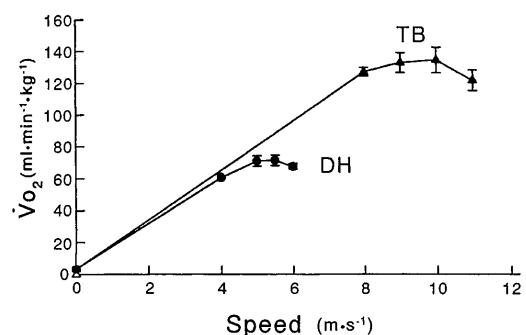

Fig. 4. Mean $\dot{V}_{O_2}$ (±SE) determined at a draft force of 10% of body weight for TB and DH. $\dot{V}_{O_2}$ was not significantly different at 8, 9, 10, and 11 m/s for TB; $\dot{V}_{O_2}$ was not significantly different at 5, 5.5, and 6 m/s for DH.

Table 2. $\dot{V}_{O_{2max}}$ and peak values of related variables for Thoroughbred and draft horses

Breed	$\dot{V}_{O_{2max}}$, ml·min^{-1}·kg^{-1}	RER	[La$^-$], mM	d[La$^-$]/dt, mM/min	[La$^-$]$_{post}$ mM	Heart Rate, beats/min
Thoroughbred	135 ± 8	1.3 ± 0.0	21.3 ± 2.1	11.9 ± 1.4	30.6 ± 1.8	217 ± 2
Draft horse	72 ± 3	1.4 ± 0.1	18.6 ± 2.1	7.4 ± 0.9	24.6 ± 1.8	201 ± 5

Values are means ± SE; n = 3 Thoroughbred and 4 draft horses, respectively. $\dot{V}_{O_{2max}}$, maximal $\dot{V}_{O_2}$. RER, respiratory exchange ratio; [La$^-$]$_{post}$, peak [La$^-$] postexercise.

times the predicted mass-specific value. Even the latter departure is greater than that of elite human athletes who achieve a $\dot{V}_{O_{2max}}$ of ~80 ml·kg^{-1}·min^{-1} (31). Aerobic capacities of ancestral equids may have been even greater than those of modern DH; that is, perhaps selective breeding for long-sustained submaximal exercise tasks has actually reduced the aerobic capacity of DH below that of ancestral equids.

Such breed differences in aerobic capacity exist within at least one other species. Greyhounds can reach $\dot{V}_{O_2}$ of 182 ml·min^{-1}·kg^{-1} (R. L. Pieschl, personal communication), 1.2–1.6 times the $\dot{V}_{O_{2max}}$ of mongrel dogs of similar weight and of unconditioned and conditioned foxhounds (113 and 146 ml·min^{-1}·kg^{-1}, respectively) (24). We know of no such great differences in aerobic capacity among breeds of mammals within a single species except where selective breeding for high exercise capacity by humans has been a major influence. Thus we suggest that the differences are results of the selective breeding and that they, and the anatomic and physiological differences that support them, reflect the nature, rate, and extent of the adaptations so achieved.

Force-speed relationships. We expected, and found, that TB could run faster than DH. We were surprised, however, to find that they could do so while exerting the same range of draft forces as DH. We were able to study draft forces only up to 20% of body weight; this limit was set in DH because our treadmill did not run at the necessary low speeds (<2 m/s) and in TB because they became agitated if asked to exert greater force. DH are capable of exerting draft forces of 100% of their body

weight at very low speeds (5); we do not know whether TB could do the same. The force-speed curves of the two breeds appear to converge as force increases, so perhaps their force intercepts are not very different.

These whole animal, maximal external force-speed curves (Fig. 5) for TB and DH resemble maximal force-velocity curves of fast and slow skeletal muscles having different maximal contraction velocities and similar maximal isometric tensions (4, 39). Musculoskeletal adaptations of TB and DH to exercise with different force-speed requirements may consist largely of differences in the intrinsic properties of their locomotor muscles, although gross anatomic differences yielding different mechanical advantages (18), or different muscle masses or recruitment patterns, also may exist in the two breeds.

Power and efficiency. We mention three salient points here. First, $\dot{W}_{max}$ of TB was twice that of DH (Fig. 5). Second, the associated $\dot{V}_{O_2}$ was also about twice as great in TB, so maximum gross efficiencies were similar in the two breeds, reaching ~20% (Fig. 7) and approaching the maximum of ~25% that is achievable by mammals. Third, maximum power and efficiency were reached at lower speeds in DH than in TB (Figs. 6 and 7). Again, these differences could arise from different intrinsic properties of the skeletal muscles in these breeds. In muscles with similar maximal isometric tensions, those with lower maximum contraction velocities necessarily have lower maximum power and reach
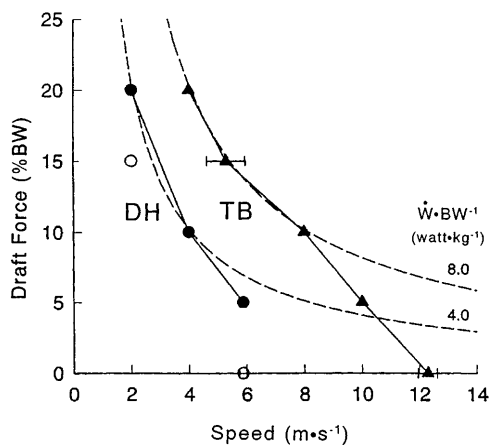

Fig. 5. Peak force-speed combinations for TB (▲) and DH (●) with power isopleths (dashed lines) of 4 and 8 W/kg. Because DH reached same speed at forces of 0 and 5 and 15 and 20% body weight (BW), points at forces of 0 and 15% BW were considered submaximal (○). $\dot{W}$, external power. Difference in peak speed between TB and DH was significant at all forces. $P \le 0.05$.
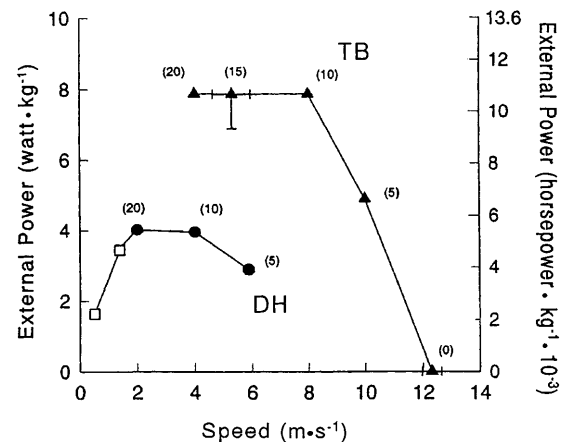

Fig. 6. Maximal mass-specific external power as a function of speed for TB and DH. Maximal external power for TB was not different at speeds of 4, 6, and 8 m/s and for DH at speeds of 2 and 4 m/s but did differ between breeds in its magnitude and speed at which it was reached. Most SE bars lie within symbols. Nos. in parentheses, draft forces (%BW) sustained at given speed; □, data obtained by Procter et al. (28) from 1 DH at speeds of 1.4 m/s exerting a draft force of 26% BW, and 0.5 m/s exerting a draft force of 33% BW.

it at lower speeds. Furthermore, maximum efficiencies will tend to occur at lower speeds in the slower muscle.

Thus, with regard to the O_2 sink, all the differences mentioned above (higher speeds, aerobic rates, and external powers in TB and the higher speeds at which they achieved maximum power and efficiency) are explainable on the basis of a single adaptive mechanism, i.e., different maximal contraction velocities (different myosin ATPase activities) of the locomotor muscles used by the two breeds in our experiments. This explanation is compatible with the idea that both breeds recruited the same muscles for maximal exercise tasks, but these muscles had very different force-speed characteristics. To optimize performance of tasks having different force-speed requirements, some animals recruit different muscles (or muscle portions) having correspondingly different force-velocity characteristics (1, 30). Our results do not suggest that this mechanism operates in TB or DH or explains differences in their performance.

We also might expect to find a higher proportion of fast-twitch oxidative fibers in locomotor muscles of TB compared with DH. Indeed, the semitendinosus muscle of TB has a higher percentage of fast-twitch oxidative glycolytic fibers than that of DH and a lower proportion of slow-twitch fibers (11). That such differences may be genetic is suggested by the fact that they exist in untrained 2-yr-old fillies (35).

The cost of locomotion is influenced by the time course of muscle force development and length changes (29, 38). We did not measure these and related variables (17) and cannot directly evaluate the extent to which elastic energy storage and recovery occurred in the two breeds at our various force-speed combinations (3, 23). We thought that if elastic properties of relevant structures (e.g., muscle-tendon units) differ in TB and DH, then different stride frequencies and $\dot{V}O_2$ might be

Fig. 8. Relationship of stride frequency to stride length as speed and draft force increased in TB (solid symbols) and DH (open symbols). Circles, data at no draft force; triangles, data for TB at a draft force equal to 20% BW. Data for DH at a draft force equal to 20% BW are omitted to preserve clarity. Data from only 2 DH at speed of 8 m/s are included, even though they could not complete 3 min at that speed.

seen in at least some of the force-speed combinations we tested. We found, however, that the O_2 cost of locomotion (i.e., the slope of mass-specific $\dot{V}O_2$ as a function of speed) (32) was not different for the two breeds (Fig. 3). In addition, stride frequencies were the same in the two breeds during trot, with draft forces of 0 and 5% of body weight. Taken together, these similarities suggest similar elastic energy storage and recovery in the two breeds under these circumstances.

On the basis of their body weights and an assumption of elastic similarity (22) in TB and DH, one would predict that stride frequencies of TB during the gallop would be 5% greater than those of DH; instead, we found a difference of 9.5% at 8 m/s. This discrepancy is not surprising; there is little reason to suggest that the breeds are elastically similar, and presumably the lighter structures of TB have higher natural frequencies than those of DH, allowing higher stride frequencies (36) and constituting an adaptation for higher running speeds.

In summary, we found that TB can run about twice as fast as DH while exerting the same range of draft forces and achieving about twice the $\dot{V}O_2$ (and $\dot{V}O_{2max}$) and external power (all scaled to body weight), with the same maximum gross efficiencies in draft work, and that maximum power and efficiency are reached at lower speeds in DH than in TB.

We suggest that these differences are largely explainable by different force-velocity characteristics in the locomotor muscles of the two breeds, attributable to genetic differences resulting from task-specific selective breeding, in TB for high-intensity exercise in high-speed tasks with low external forces and in DH for low-intensity exercise in low-speed tasks with high external forces. Associated adaptations of gas-exchange and -transport mechanisms can be expected.
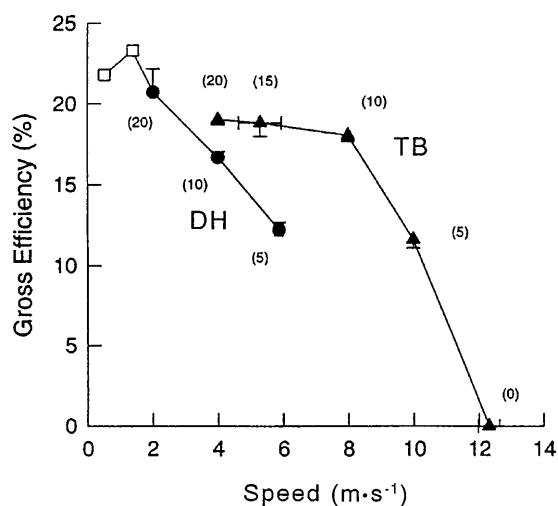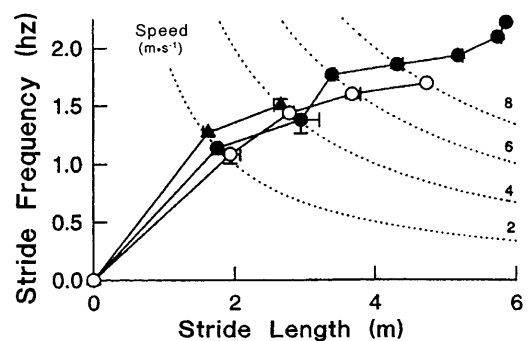

Fig. 7. Relationship of gross efficiency and speed for TB and DH while exerting peak sustainable draft forces (%BW in parentheses) at a given speed. Gross efficiency was not significantly different for TB at speeds of 4, 6, and 8 m/s but was significantly different for DH at all speeds studied. Between breeds, speed at which maximal gross efficiency occurred was significantly different, but maximal gross efficiency was not. Open symbol is defined as in Fig. 6. $P \le 0.05$.

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