

The physiology of rowing

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Abstract

Rowing competitions for males are performed over a distance of 2000 m and last 5.8–7.4 min. This time is being improved by 0.01 min per year. Races are most often carried out with an initial spurt in order to increase the total aerobic metabolism. Large individuals have an advantage partly because of a larger anaerobic metabolism, but also because the almost constant weight of the boat, oars and coxswain becomes relatively less for oarsmen with larger body dimensions. Oxygen uptake during rowing increases with velocity to the power 2.4. It is estimated that the metabolic cost of rowing at racing speed corresponds to $6.4 \text{ l O}_2 \text{ min}^{-1}$. The most successful oarsmen have a weight of $93 \pm 2.6 \text{ kg}$ ($\pm \text{s.e.}$) and a maximal oxygen uptake of $5.9 \pm 0.08 \text{ l min}^{-1}$ ($\pm \text{s.e.}$). A direct relationship is demonstrated between the average maximal oxygen uptake of the crew (y) and their placing (x) in an international regatta, $y = 6.15 - 0.08x$ ($r = 0.87$). In contrast, measures of muscle strength do not separate the good from less qualified oarsmen except that the best oarsmen can develop a larger force in a simulated rowing position (2000 N). Maximal oxygen uptake is greater during rowing than during running or bicycling, probably because of the intensive involvement of a larger muscle mass. The capacity of the oxygen transporting system is shown to be dependent on the local (muscle) blood flow. Thus metabolic, circulatory and strength measurements indicate that training for rowing should simulate rowing in the boat as much as possible.

Keywords: Aerobic metabolism, anaerobic metabolism, body dimensional influence on work capacity, limiting factors for performance, muscle strength, rowing physiology.

Introduction

A first attempt to describe the physiology of rowing was carried out when Liljestrand and Lindhard (1920) measured oxygen uptake, heart rate and cardiac output during rowing of an 'ordinary' boat. Henderson and Haggard (1925) estimated the energy expended in rowing an eight-oared racing shell by the determination of (a) the pull when the boat was towed by a motor boat; (b) the work performed during rowing a machine; and (c) the volume of oxygen consumed from the air by the oarsmen's breathing. At very low velocities Ewig (see Törner, 1959) determined oxygen uptake during rowing a racing shell.

Since then experiments have focused mainly on the determination of the maximal oxygen

uptake of oarsmen (Mellerowicz and Hansen, 1965; Saltin and Åstrand, 1967; Nowacki *et al.*, 1969, 1971; de Pauw and Vrijens, 1971; Bloomfield and Roberts, 1972; Secher *et al.*, 1974, 1982a,c; Asami *et al.*, 1978), and a comparison has been made with values obtained during other types of exercise (Strydom *et al.*, 1967; Carey *et al.*, 1974; Jackson and Secher, 1976; Cunningham *et al.*, 1975; Strømme *et al.*, 1977; Larsson and Forsberg, 1980). Of special interest for oarsmen is the importance of arm work in the maximal oxygen uptake of the subject (Åstrand, 1952; Taylor *et al.*, 1955; Åstrand and Saltin, 1961a; Andersen *et al.*, 1961; Stenberg *et al.*, 1967; Kamon and Pandolf, 1972; Hermansen, 1973; Gleser *et al.*, 1974; Secher *et al.*, 1974, 1977; Reybrouck *et al.*, 1975; Secher and Oddershede, 1975; Bergh *et al.*, 1976; Strømme *et al.*, 1977).

Oxygen deficit and debt of oarsmen have also been measured (Asami *et al.*, 1978; Hagerman *et al.*, 1978, 1979; Secher *et al.*, 1982a), as has their strength (Yamakawa and Ishiko, 1966; Bloomfield and Roberts, 1972; Hagerman *et al.*, 1972; Secher, 1975; Larsson and Forsberg, 1980), and values have been presented for muscle histochemistry (Bonde-Petersen *et al.*, 1975; Larsson and Forsberg, 1980; Secher *et al.*, 1981), vital capacity (Yamakawa and Ishiko, 1966), heart volume (Mellerowicz and Hansen, 1965), and echocardiographic measurements of ventricular volume and wall thickness (Howald *et al.*, 1977; Keul *et al.*, 1982). These variables have been followed during training for competitive rowing (Schausen, 1965; Larsson and Forsberg, 1980; Secher *et al.*, 1982a) and have been related to rowing performance (Yamakawa and Ishiko, 1966; Hagerman *et al.*, 1972, 1975; Bloomfield and Roberts, 1972; Asami *et al.*, 1978; Larsson and Forsberg, 1980; Secher *et al.*, 1982e).

Representative racing results in international championship regattas arranged by the Fédération Internationale des Sociétés d'Aviron (FISA) have been calculated (Secher, 1973) and the force applied on the oar has been determined (Ishiko, 1968; Hagerman and Lee, 1971; Schnedier *et al.*, 1978; Asami *et al.*, 1978) allowing a calculation of the minimum work performed by the oarsmen at various rowing speeds (Celentano *et al.*, 1974). The investigations have also involved an estimate of the metabolic cost of rowing (di Prampero *et al.*, 1971; Jackson and Secher, 1976). The studies have most often involved male heavyweight rowers. Thus few values exist for women and lightweight rowers (Hagerman *et al.*, 1979; Secher *et al.*, 1982a). Some biomechanical (Nigg, 1977) and physiological (Törner, 1959; Åstrand and Rodahl, 1977; Reilly, 1981) aspects of rowing have been reviewed in textbooks, and a monograph on biomechanical aspects of rowing has appeared (Schneider, 1980).

The measured variables are most often large, for example, maximal oxygen uptake in excess of 61 min^{-1} (STPD), and can be difficult to evaluate as most physiological measures are dependent upon body dimensions (Asmussen and Heebøll-Nielsen, 1955; Åstrand and Rodahl, 1977; Asmussen *et al.*, 1981) and oarsmen are usually large individuals (Hirata, 1979). Another problem has been to explain why heavyweight oarsmen row faster than lightweight ones row (McMahon, 1971).

Rowing is different from most other types of human exercise owing to the fact that the body is supported by a seat, and also because of the involvement of both arms and legs, the two legs working in the same phase. This contrasts with running, for example, during which one leg is predominantly performing work at a time.

This paper describes some aspects of rowing physiology with special reference to the influence of body size on rowing performance and on the measured variables, and to the metabolic cost of

rowing. Some neural and circulatory problems involved when several muscle groups are working simultaneously are also considered.

Rowing competitions

Rowing competitions are performed over a distance of 2000 m for men and 1000 m for women. Races are held for boats in which each rower uses two sculls and in boats where each oarsman handles one larger oar. Fours and pairs may or may not include a coxswain while the single scull is rowed without one. The eights do have a coxswain. Men's events are held separately for lightweights. They may also compete in an open class. The lightweights are allowed a maximum weight of 72.5 kg and an average weight of 70 kg.

Open-class international rowing championships (European, one North American in 1967, world and Olympic) have been arranged by FISA since 1893. Olympic regattas were introduced in 1900. For women, FISA championships have taken place since 1954 and women have participated in the Olympic Games since 1976. 'Unofficial' lightweight championships were held for the first time in 1974.

Since the first regatta took place the mean results in the men's open class have improved by about 0.01 min per year (Fig. 1, Table 1, Secher, 1973), while differences in lane and wind circumstances do not allow yet for the detection of significant improvement in results obtained by women and lightweight rowers.

The median of the results obtained in FISA regattas from 1974 to 1982 indicates a race duration in the men's open class of 6.6 min, while the median rowing time for women is 3.4 min, and 6.6 min for lightweights (Table 2). The values presented in Table 2 indicate a difference in

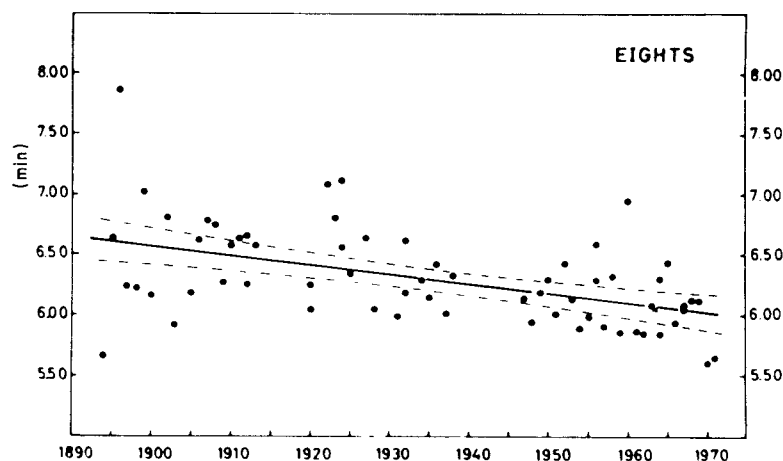


Fig. 1. Results obtained by FISA regatta winning eight-oared crews over 2000 m 1893 to 1971. The regression line and its 95% confidence limits are shown. This figure is published with the kind permission of the American College of Sports Medicine.

Table 1. Regression lines between winning results in FISA regattas and the year of the regatta (1979 is the last year included in the calculations). Boat type indicated with the number of oarsmen, plus or minus a coxswain, an x indicates a sculler. The year of the first regatta and the correlation coefficient (r) are also shown.

Boat type	First regatta	Regression line ^a	r	P
4+	1893	$Y = -0.0129X + 7.538$	0.69	^b
2-	1920	$Y = -0.0140X + 8.106$	0.54	^b
1x	1893	$Y = -0.0113X + 8.140$	0.57	^b
2+	1893	$Y = -0.0124X + 8.460$	0.60	^b
4-	1924	$Y = -0.0097X + 7.148$	0.49	^b
2x	1898	$Y = -0.0109X + 7.524$	0.65	^b
8+	1893	$Y = -0.0092X + 6.622$	0.57	^b

^a The year 1900 was chosen as the starting point, Y = winning time in min, X = year of regatta, i.e. 70 for 1970.

^b Indicate $P < 0.001$.

results obtained by heavyweights and lightweights of 2.5% in comparable events, supporting the impression that a large body weight is an advantage.

The influence of body dimensions on rowing performance*

According to Hill (1927) the total energy expenditure (E) during an exhausting athletic event may be expressed as

$$E = S + \Delta R t \quad (1)$$

where S represents an expendable energy store, ΔR is the maximal possible increase in metabolic rate above the resting value, and t is the duration of the event.

The energy store corresponds to the sum of energy that can be transformed by hydrolysis of adenosine triphosphate and creatine phosphate (CP), by oxidation using a large part of the oxygen bound to haemoglobin and myoglobin, and by anaerobic splitting of glycogen to give lactate. Thus S may represent the 'oxygen deficit' developed during the event.

The variables making up S are all volume dependent and must therefore be expected to increase in proportion to the power three of a characteristic linear dimension (p) of the subject. Total myoglobin, glycogen, CP etc. are proportional to muscle mass, which again is proportional to p^3 . As the distribution volume for lactate also is proportional to p^3 it follows that, for example, blood lactate concentration after maximal exercise should be equal in large and small individuals (Fig. 2, Secher *et al.*, 1983).

ΔR represents aerobic power, i.e. the energetic ('caloric') value of the volume of oxygen used

* Secher and Vaage, unpublished work.

Table 2. Observed results in rowing (median of winning times in FISA championships 1974-82). Also given are the calculated racing results based on Equations 7 and 9 using the constants developed and matched to the results obtained in the single scull and coxed fours in order to obtain a mechanical efficiency (*me*) for the equations. Boat velocity and time equivalent of one boat length are also given.

Event	Boat type ^a	Racing time (min s)		Velocity	$s \times (\text{boat length})^{-1}$
		Observed	Calculated		
Men	1x	7 10		4.65	1.72
	2x	6 36	6 36	5.05	2.08
	4x	5 57	6 04	5.60	2.32
	2-	7 01	6 55	4.75	2.21
	2+	7 22	7 14	4.52	2.43
	4-	6 17	6 22	5.31	2.45
	4+	6 30		5.13	2.73
	8+	5 45	5 55	5.80	3.19
Median		6 36		5.05	2.38
Women	1x	3 47		4.40	1.82
	2x	3 24	3 28	4.90	2.14
	4x+	3 20	3 15	5.00	2.80
	2-	3 43	3 35	4.48	2.45
	4+	3 21		4.98	2.81
	8+	3 05	3 02	5.41	3.42
Median		3 23		4.94	2.80
Leighweights	1x	7 20	7 21	4.54	1.76
	2x ^b	6 39	6 46	5.01	2.09
	4-	6 30	6 32	5.13	2.54
	8+	5 57	6 05	5.60	3.30
Median		6 35		5.07	2.32

^a For symbols, see Table 1.

^b First regatta 1977.

per unit of time. Maximal aerobic power is equal in both large and small well-trained athletes when related to body weight to the power 2/3 (Vaage and Hermansen, 1977; Secher *et al.*, 1983; Table 3). This result is expected since, in physiological events, time can be shown to correspond to a linear body dimension (Asmussen *et al.*, 1981). Aerobic power, therefore, must be expected to increase in proportion to $p^3 \times p^{-1} = p^2$ (or to $\text{weight}^{2/3}$). The influence of body dimensions on *E* may be expressed accordingly as

$$E = k_a p^3 + k_b p^2 t \quad (2)$$

or

$$E = k_1 w + k_2 w^{2/3} t \quad (3)$$

where *w*, the body mass is assumed to be proportional to p^3 , and the *k* values are constants.

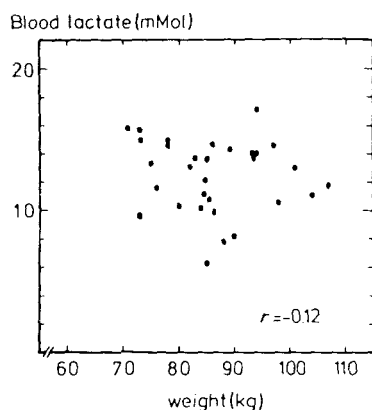


Fig. 2. Blood lactate concentrations after maximal bicycle or treadmill exercise plotted against body weight.

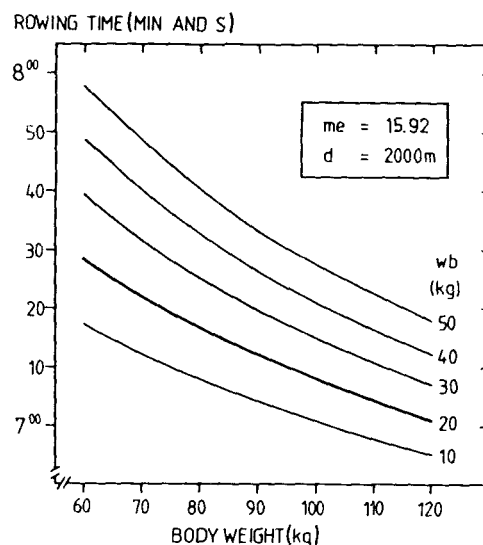


Fig. 3. Relationship between the calculated duration of rowing over 2000 m for men and the weight of the oarsman. The thick line represents results calculated using the approximate weight (w_b) per oarsman of coxless boats.

The mean boat resistance to progression (BR) increases in proportion to the velocity of the boat (v) to the power 1.95 (Celentano *et al.*, 1974). BR is also dependent on the total load carried by the boat, w_b , i.e. the weight of the rower and the weight of the boat, rigging and oars. This dependency can be calculated for the single scull from the data of Balukow (1964) to be proportional to $(w + w_b)$ to the power 0.56 at racing speed and within the range of displacements measured, 80–120 kg. Thus

$$BR = k_3 v^{1.95} (w + w_b)^{0.56} \quad (4)$$

At constant boat velocity the work (W) performed by the oarsman is BR times the distance rowed (d), that is, $W = BR \times d$ and E is balanced by W through the mechanical efficiency (me):

$$E \times me = BR \times d \quad (5)$$

for which an 'allometric' expression (Huxley and Teissier, 1936, see Asmussen *et al.*, 1981) according to the above is

$$(k_1 w + k_2 w^{2/3} t) me = k_3 v^{1.95} (w + w_b)^{0.56} d \quad (6)$$

Table 3. Average values \pm s.e. for age, height, weight, per cent fat and maximal values of heart rate (HR_{\max}), oxygen uptake ($\dot{V}O_2 \max$), oxygen pulse and ventilation ($\dot{V}_E \max$) in winners of international rowing competitions and their less successful counterparts.

	Age (years)	Height (cm)	Weight (kg)	Fat (%)	HR_{\max} (min^{-1})	$\dot{V}O_2 \max$ (l min^{-1})	$\dot{V}O_2 \max$ ($\text{l min kg}^{-2/3}$)	$\dot{V}O_2 \max$ ($\text{ml kg}^{-1} \text{min}^{-1}$)	Maximum oxygen pulse ($\text{ml } HR^{-1}$)	$\dot{V}_E \max$ (l min^{-1})
<i>Winners of international rowing championships (n=14)</i>										
Mean	25.6	192	93	6.5	185	5.89	288	63	32	200
\pm s.e.	0.58	1.5	2.6	0.54	2.5	0.076	4.9	1.5	0.7	7.1
<i>Internationally competing oarsmen (n=13)</i>										
Mean	25.1	189	84	8.3	190	5.58	291	67	29	173
\pm s.e.	0.47	1.1	1.8	0.43	3.0	0.064	4.7	1.4	0.6	3.8
t values	0.6685	1.3007	2.7281 ^b	-2.3097 ^a	1.2997	3.0847 ^b	0.4418	1.6885	2.6575 ^b	3.2405 ^c

^a $P < 0.05$.

^b $P < 0.02$.

^c $P < 0.005$.

and as, at constant boat velocity, $v = dt^{-1}$

$$t^{1.95}(k_1w + k_2w^{2/3}t)me = k_3(w + wb)^{0.56}d^{2.95} \quad (7)$$

Equation 6 can be modified to include the number of rowers (n) in the boat. Thus the energy expenditure will increase with the number of oarsmen, and so will the resistance:

$$n(k_1w + k_2w^{2/3}t)me = k_3v^{1.95}[n(w + WB)]^{0.56}d \quad (8)$$

where WB is taken to mean the weight of the boat, rigging and coxswain per oarsman, and it is assumed that boat resistance increases with an increase in displacement as for the single scull. Equation 8 may be written as:

$$n^{0.44}t^{1.95}(k_1w + k_2w^{2/3}t)me = k_3(w + WB)^{0.56}d^{2.95} \quad (9)$$

or

$$n^{0.44}(k_1w + k_2w^{2/3}t)me = k_3v^{1.95}(w + WB)^{0.56}d \quad (10)$$

Accepting McMahon's (1971) assumption that the boat weight per oarsman and the body weight per oarsman are constant, and disregarding the anaerobic metabolism, Equation 10 can (since $dt^{-1} = v$) be reduced to the formula derived by McMahon (1971)

$$v = k_4n^{0.15} \quad (11)$$

in which k_2 , k_3 , $w^{2/3}$, $(W + Wb)^{0.56}$ and me make up the new constant k_4 . Thus for boats of similar construction and with their weight (including a cox) proportional to the number of oarsmen, the boats containing many oarsmen should go faster than those containing fewer oarsmen. Taking as an example the results for the eights and the pairs (Table 2), the difference in time at the finishing line amounts to 22% [16% from the regression lines (for 1979), and 6% for women] while the prediction from Equation 11 would be 23%.

For the application of Equations 7 and 9, the constants k_1 and k_2 can be calculated from the energy equivalents of the measured oxygen deficit $E(OD)$ and total oxygen uptake $E(VO_2)$ during 'all-out' exercise on a rowing ergometer

$$E(OD) = k_1w \quad (12)$$

and

$$E(VO_2) = k_2w^{2/3}t \quad (13)$$

In seven male oarsmen (Secher *et al.*, 1982a) with an average weight of 82 kg, the mean value of OD was 4.8 l O_2 and the mean value of VO_2 was 30.2 l during a row of 6 min on a Gjessing ergometer. These values give a k_1 value of about 1200 J kg^{-1} and a k_2 value of about 91 J $kg^{-2/3} s^{-1}$.

In four female rowers with an average weight of 66 kg, OD was 4.2 l O_2 and VO_2 was 14.0 l for 4 min of maximal rowing (Secher *et al.*, 1982a). Thus, k_1 was found to be about 1340 J kg^{-1} and k_2 to be about 73 J $kg^{-2/3} s^{-1}$.

k_3 may be calculated from the data of Balukow (1964) for the single scull to be 0.263 N $kg^{-0.56}v^{-1.95}$.

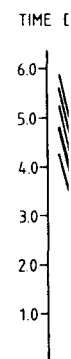


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w_b and W_B are found from the minimum boat weight including rigging allowed by FISA, the weight of the oars, and the weight of the coxswain (50 kg for men and 40 kg for women).

The mechanical efficiency during rowing is not known but may be expected to be low, because 22% or more of the energy is used in a direction transverse to the direction of the boat (Celentano *et al.*, 1974). Equation 7 will fit the results obtained in FISA regattas for the single scull if a mechanical efficiency of 15.92% is assumed (Fig. 3, Table 2).

Taking as an example an increase in body weight of a male rower of 10 kg, the use of the allometric expression for rowing, Equation 7, indicates a 1.1% per 10 kg time advantage for the heavier rower. The calculated value for body weights of 70 and 93 kg indicates an advantage for heavyweights of 2.6% over a rowing distance of 2000 m (Fig. 4, $w_b = 20$ kg).

The calculated average disadvantage of carrying an extra boat weight of 10 kg per oarsman, for example, due to a difference in boat construction and rigging, or due to a coxswain, amounts to 1.6% (Fig. 3). The observed value on average is also 1.6% per 10 kg per oarsman when the results of coxed and coxless pairs and fours (Table 2) are compared.

The calculations may have significant implications. Females row fours and quad scull boats with a coxswain rather than a coxless boat. Therefore they move a boat weight per rower of 28 kg instead of 18 kg. Using Equation 9 with the constants developed for females it is calculated that if women row coxless boats, the advantage of a 70 kg over a 60 kg female would be reduced from 2.1 to 1.8%. Furthermore if women were to row 2000 m as men do, the advantage of the 10 kg heavier athlete would be reduced to 1.5%.

In conclusion, the larger anaerobic capacity (oxygen deficit) of heavyweights provide them

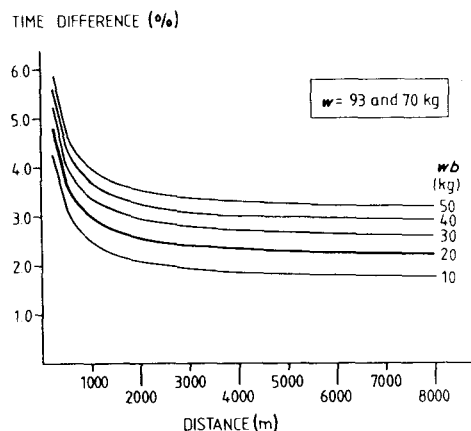


Fig. 4. Calculated time differences between rowing results of heavyweight (average weight 93 kg) and lightweight (average weight 70 kg) oarsmen and the distance rowed. The calculations are based on Equation 7 assuming that k_1 and k_2 are independent of the duration of the event. The thick line is the same as in Fig. 3.



Fig. 5. Experimental set up for collecting expired air during rowing. This figure is published with the kind permission of the American College of Sports Medicine.

with an advantage during rowing which is accentuated because any given weight of a boat, oars, rigging and coxswain is relatively less for an athlete with larger body dimensions.

The metabolic cost of rowing†

The relationship between heart rate and oxygen uptake during rowing in a tank has been used to estimate the metabolic cost of rowing by the determination of the heart rate during rowing (di Prampero *et al.*, 1971). A more direct approach is to measure the oxygen uptake during rowing using Douglas bags (Fig. 5, Jackson and Secher, 1976; Strømme *et al.*, 1977).

Using the Douglas bag method, values were determined during steady-state rowing on a canal on days with calm water for two experienced oarsmen with weights of 79 and 92 kg, respectively. In the single scull, velocities between 2.1 and 4.9 m s⁻¹ were used, in the double sculls the velocities were between 2.4 and 4.9 m s⁻¹, and in the coxless pairs the velocities were between 2.4 and 5.1 m s⁻¹ (Figs. 6–8).

Oxygen uptake ranged between 1.21 and 4.87 l min⁻¹ for one oarsman and between 1.53 and 6.45 l min⁻¹ for the other. The resting value was 0.28 l min⁻¹. The results obtained for the two subjects were treated as one sample. In order to reduce the influence of the anaerobic metabolism on the results at the greatest speeds ('flattening' out of the curves), only oxygen uptake values which were lower than 95% of the highest recorded value were used for the calculations (Figs. 6–8).

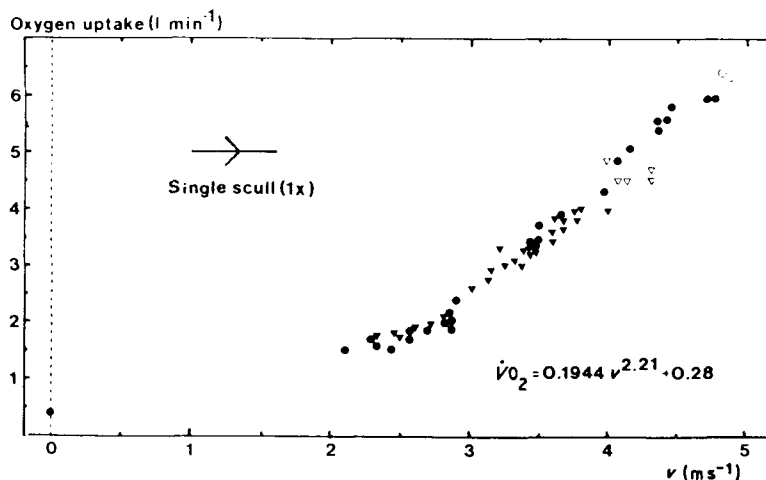


Fig. 6. Oxygen uptake during rowing a single scull in two subjects. Values indicated with open symbols were not used in the regression.

† Some of these results have been presented in another form by Jackson and Secher (1976) and Åstrand and Rodahl (1977).

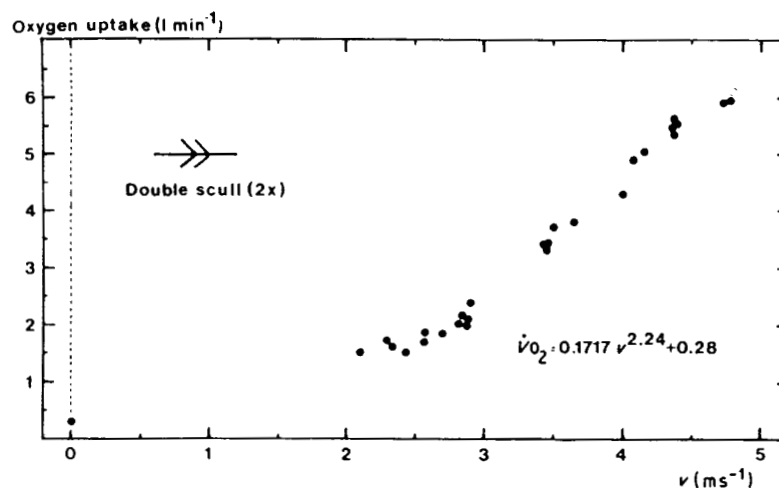


Fig. 7. Oxygen uptake during rowing a double scull. For symbols see Fig. 6.

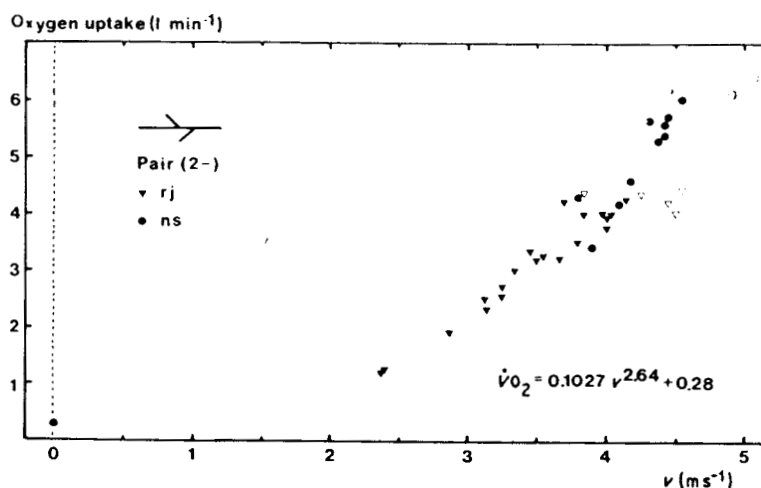


Fig. 8. Oxygen uptake during rowing a coxless pair in two subjects. For symbols see Fig. 6.

For the coxed pairs, boat resistance to progression is found to follow the equation

$$BR = av^b \quad (14)$$

where a has a value of $4.7 \text{ kg m}^{-0.95} \text{ s}^{-0.05}$ and b has a value of 1.95 (Celentano *et al.*, 1974; cf. Equation 4).

The relationship between oxygen uptake and rowing velocity is also expected to be a power function, but the rate of oxygen uptake, being a measure of power, or force \times velocity, is

according to Equations 4 and 5 expected to increase with velocity to the power 2.95. Expressing oxygen uptake as a power function of v , then

$$\dot{V}O_2 = a^1 v^{b^1} + c \quad (15)$$

where c is the rate of oxygen uptake at rest. Subtracting c on both sides allows for the logarithmic expression

$$\log(\dot{V}O_2 - c) = \log a^1 + b^1 \log v \quad (16)$$

which is a straight line with a slope b^1 and intercept $\log a^1$. Thus the constants a^1 and b^1 may be determined experimentally from measured oxygen uptake at various rowing velocities.

For the three boat types studied the following equations were developed (Figs. 6–8)

$$\text{Single scull: } \dot{V}O_2 = 0.194 v^{2.21} + 0.28 \quad r = 0.98 \quad (17)$$

$$\text{Double sculls: } \dot{V}O_2 = 0.172 v^{2.24} + 0.28 \quad r = 0.98 \quad (18)$$

$$\text{Pairs: } \dot{V}O_2 = 0.103 v^{2.64} + 0.28 \quad r = 0.98 \quad (19)$$

where r is the correlation coefficient. Oxygen uptake is measured in l min^{-1} and boat velocity in m s^{-1} .

Oxygen uptake was also determined during 'no-load' tank rowing using a frequency of 20, 30 and 40 strokes per minute (Fig. 9). This was done in order to separate the oxygen uptake used for boat progression from the total oxygen uptake by subtracting the oxygen uptake found during no-load rowing at the applied number of strokes per minute (Fig. 10). Accordingly, the oxygen uptake used for boat progression was found to be

$$\text{Single scull: } \dot{V}O_2 = 0.060 v^{2.60} \quad r = 0.93 \quad (20)$$

$$\text{Double sculls: } \dot{V}O_2 = 0.030 v^{3.14} \quad r = 0.95 \quad (21)$$

$$\text{Pairs: } \dot{V}O_2 = 0.013 v^{3.57} \quad r = 0.97. \quad (22)$$

On average the total rate of oxygen uptake increased with the velocity to the power 2.4 (Equations 17–19) while the estimated oxygen uptake used for boat progression (Equations 20–22) increased with a mean boat velocity to the power 3.1, i.e. close to the expected value of 2.95.

Using the equations developed for the total oxygen uptake during rowing (Equations 17–19) and the rowing results presented in Table 2, the metabolic cost of rowing at racing speed can be calculated to be an average of 6.38 l min^{-1} (for 1979, Table 4). Corresponding values can be calculated for previous years using the equations describing the relationship between rowing results and the year of the regatta (Table 1). It appears (Table 4) that the metabolic cost of rowing at racing speed has increased progressively with a value of 190 ml min^{-1} between 1919 and 1929, but 240 ml min^{-1} between 1969 and 1979.

Hendersson and Haggard (1925) estimated that the metabolic cost of rowing at racing speed was about $6.1 \text{ l O}_2 \text{ min}^{-1}$ (30 kcal min^{-1}) in 1924, while the estimate from Table 4 would be $5.2 \text{ l O}_2 \text{ min}^{-1}$. However, their greatest measured oxygen uptake was only 4.3 l min^{-1} , and only one subject attained a work output of about 420 W. This, however, was over a period

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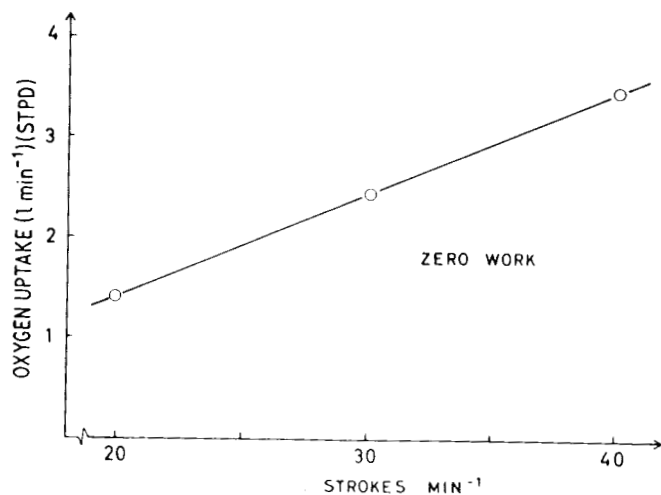


Fig. 9. Oxygen uptake during 'no-load' tank rowing.

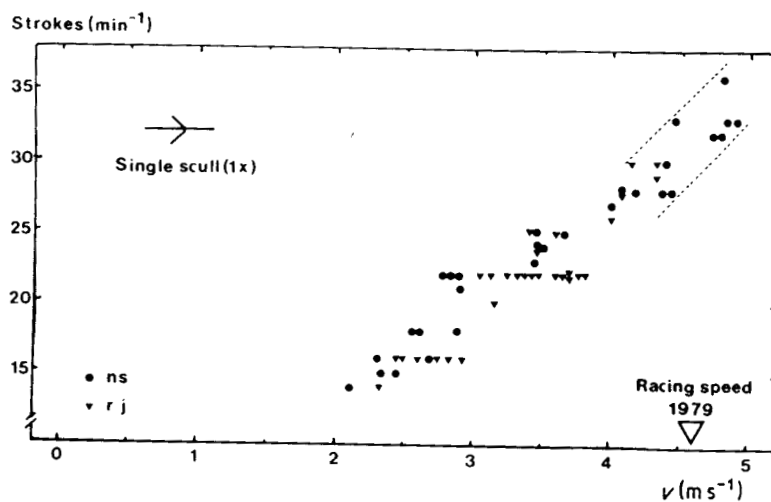


Fig. 10. Number of strokes used per minute (rating) during rowing a single scull in two subjects. Calculated racing speed (for 1979) is indicated.

limited to 3 min, whereas the duration of a race in the eights would be expected to be 6.4 min in 1924 (Table 1).

According to Equation 14 the power of rowing at racing speed in the coxed pairs (in 1979, Table 1) is 386 W in the direction of the boat, or a total work output of 471 W if 22% (or more) of the work is in a transverse direction (Celentano *et al.*, 1974). Accepting a metabolic cost of rowing at racing speed of about 6.38 l min^{-1} , the mechanical efficiency of rowing should be 22%.

Table 4. Calculated metabolic cost of rowing at racing speed in FISA championships 1919-79.

	1919	1929	1939	1949	1959	1969	1979
Metabolic cost (l O ₂ min ⁻¹)	5.10	5.29	5.48	5.69	5.91	6.14	6.38

Oxygen uptake during simulated race rowing

The previous considerations were made under the assumption that rowing velocity is close to constant during a race. It appears, however, that rowing velocity is greatest at the beginning of a race and then diminishes gradually during the next 1500 m to increase to near the average velocity for the final 500 m (Schneider, 1980; Secher *et al.*, 1982a, Fig. 11).

The reason for the initial spurt is not known. The most economical way to row the 2000 m would be to keep an average velocity throughout the race. One explanation could be psychological. Oarsmen are sitting with their backs towards the direction of the boat. They therefore have to be in the lead in order to see their competitors. This mechanism, however, does not explain why oarsmen row in a similar pattern when performing all-out exercise on a rowing ergometer (Hagerman *et al.*, 1978; Schneider, 1980; Secher *et al.*, 1982a).

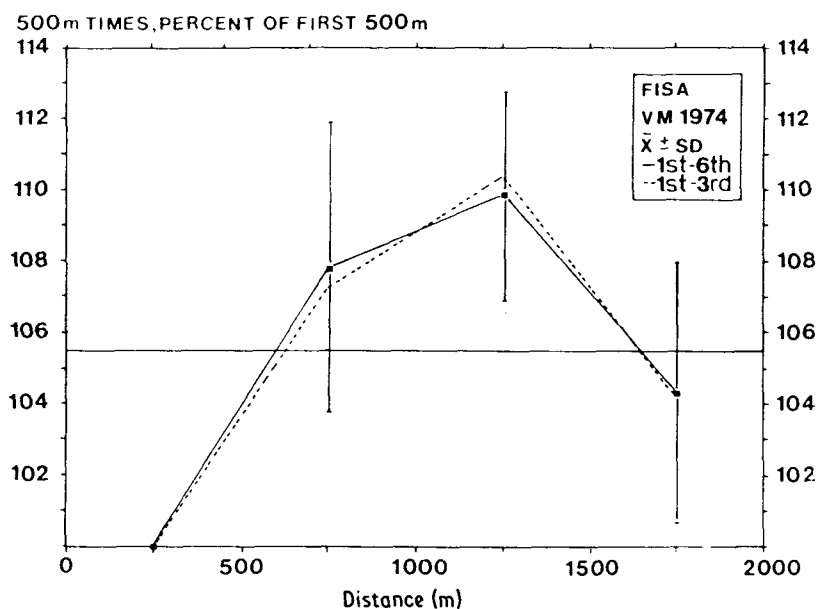


Fig. 11. Relative 500 m racing times calculated for all participants in the finals (1st to 6th place) of the 1974 world championship FISA regatta for men. Values indicated (\pm s.d.) at the 250 m marks. Also shown relative 500 times for the three first boats in each competition. Horizontal line indicates the average relative 500 m racing time.

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A physiological explanation for the initial spurt performed could be that the rate of increase in oxygen uptake at the onset of exercise is highest the greater the work load (Hill and Lupton, 1923; Furusawa *et al.*, 1924; Neukirch, 1938; Åstrand and Saltin, 1961b; Linnarsson, 1974). Accordingly, the total oxygen uptake and work output during a given period of exercise is larger when an initial spurt is performed than when one attempts to keep exercise at an average intensity throughout a race (Secher *et al.*, 1982a, Fig. 12). In this respect it is interesting that it appears the initial spurt can be performed without an increase in the total anaerobic metabolism as indicated by the size of the oxygen debt (Fig. 12) and the blood lactate concentration (Secher *et al.*, 1982a).

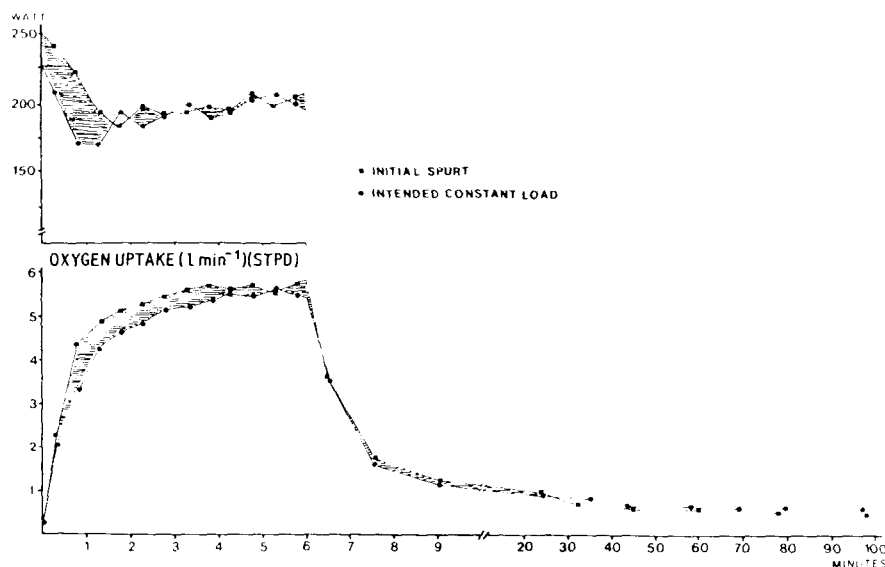


Fig. 12. Oxygen uptake followed during intense bicycle exercise of 6 min duration and for the following 100 min of rest. Values are shown with an intended constant work load procedure and during exercise performed with an initial spurt.

Contribution of the anaerobic and aerobic metabolism to rowing

There is no simple way to express the contribution of the anaerobic metabolism to exercise. The existence of an anaerobic metabolism is often assessed by measurement of blood (or muscle) lactate concentrations despite difficulties in determining the distribution volume for lactate (Margarita *et al.*, 1963; Klausen *et al.*, 1974). In oarsmen maximum blood lactate concentration has been found to be 11 mmol l⁻¹ after 'maximal' running on a treadmill, while 15 mmol l⁻¹ was obtained after a national competition, and 17 mmol l⁻¹ after a FISA championship regatta (Vaage, 1977). Thus psychological factors may influence the results. The average value for blood lactate in Fig. 2 is 12.5 ± 0.45 mmol l⁻¹ (S.E.).

Determination of an oxygen debt, i.e. the oxygen uptake above the resting value after

termination of exercise (Fig. 12) is another method of estimating anaerobic metabolism. Values of oxygen debt presented for oarsmen are based on a collection of expired gas over a period of 30 min, but this collection period is arbitrarily chosen. Values are smaller in beginners (9 l) than in well-trained oarsmen (14 l) (Asami *et al.*, 1978; Hagerman *et al.*, 1978, 1979) with a maximum value of 33 l (Secher *et al.*, 1982a). For women and lightweights, values of 10 and 12 l have been presented (Hagerman *et al.*, 1979).

'Oxygen deficit' would probably be a more accurate measure of the size of the anaerobic metabolism, but it is based on calculations rather than on direct measurements. For international calibre oarsmen values of 8 l have been published for lightweights and 6 l for women (Hagerman *et al.*, 1979), somewhat larger values than those determined by our group (Secher *et al.*, 1982). The values we determined corresponded to a 14% contribution by the anaerobic metabolism for men during 'all out' rowing for 6 min, while the contribution in 'all out' rowing in women was 23% for 4 min. These values are somewhat less than those generally expected for other types of 'all out' exercise of 4 to 6 min (Åstrand and Rodahl, 1977).

Ventilation during rowing†

It has been argued that 'the cramped position of the body while rowing should constrict the abdominal muscles and limit their ability to aid the expiratory phase of each breathing cycle' (Cunningham *et al.*, 1975). Ventilation during rowing, however, does not seem to be 'low'. As during other types of dynamic exercise (Asmussen and Nielsen, 1946; Saltin and Åstrand, 1967) ventilation increased linearly with oxygen uptake to approximately 80% of the maximal oxygen uptake (Fig. 13). With a further increase in work intensity ventilation increased exponentially to reach values of 158 and 206 l min⁻¹ (BTPS) at slightly submaximal oxygen uptakes of 4.70 and 6.25 l min⁻¹, respectively (the maximal values were 4.87 and 6.45 l min⁻¹). There appeared to be no difference in ventilation whether the subject rowed the single or double sculls. The subject reaching a ventilation of 206 l min⁻¹ during rowing had a ventilation of 243 l min⁻¹ during exhaustive bicycle exercise.

Heart rate during rowing†

Heart rate during rowing competitions has been measured (Ishiko, 1968; Pruett, 1977; Schneider, 1980; Fig. 14). Heart rate measurements have also been obtained during rowing ergometer exercise (Hagerman and Lee, 1971; Secher *et al.*, 1982a). In general these show the same maximal values as during bicycling (Hamley and Thomas, 1969; Cunningham *et al.*, 1975). To make possible a prediction of the metabolic cost of rowing, heart rate was measured at various submaximal intensities (di Prampero *et al.*, 1971). A fixed amount of oxygen consumed per minute, however, does not necessarily result in one and the same heart rate even in the same subject. It is well known that heart rate during submaximal arm exercise is higher than during leg exercise at the same pulmonary oxygen uptake (Christensen, 1931; Asmussen and

† Unpublished work carried out with Roger C. Jackson, University of Calgary, Alberta, Canada.

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Fig. 14.

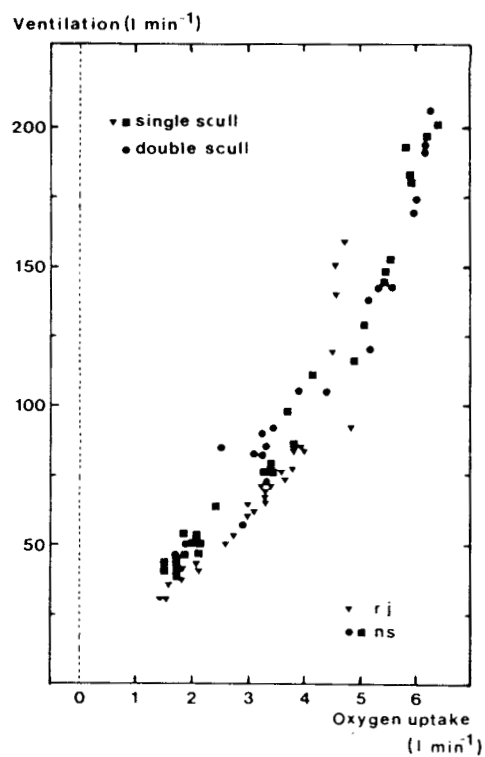


Fig. 13. Pulmonary ventilation during rowing measured in two oarsmen.

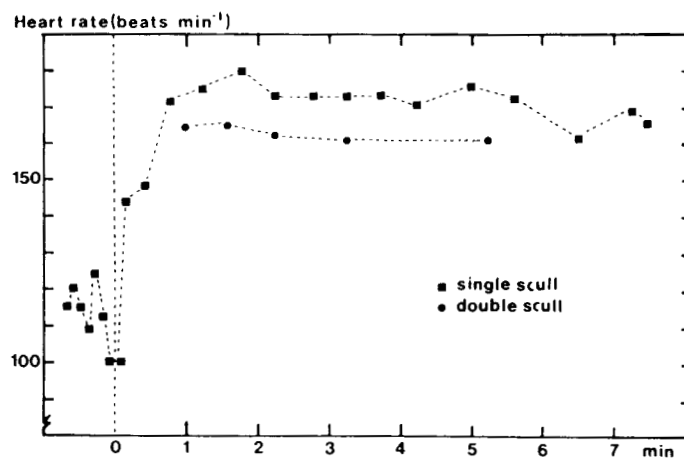


Fig. 14. Heart rate of one subject followed during race rowing in single and double sculls.

Hemmingsen, 1958; Åstrand *et al.*, 1965; Stenberg *et al.*, 1967; Vokac *et al.*, 1975). Also, the maximal heart rate seems to be dependent upon the muscle mass involved in exercise (Stenberg *et al.*, 1967; Klausen *et al.*, 1982) and may vary from one type of exercise to another, especially when repeated maximal bursts of activity are involved (Tørring, personal communication; own experience).

During race rowing heart rate was higher in the single than in the double sculls for an oarsman trained for double sculls rowing (Fig. 14). Even more surprising was the finding of a similar heart rate during bicycling and single scull rowing, but a significantly lower heart rate at a given oxygen uptake during double sculls rowing in the same subject (Fig. 15). These findings could indicate that heart rate during dynamic exercise is dependent upon the specific work situation that applies rather than on the muscle groups involved, especially when specific training is carried to an extreme as in competitive sports. The difference in heart rate response cannot be explained by a difference in the work performed per stroke in the two boat types. During bicycling heart rate is the same at a given oxygen uptake at various pedalling rates (Knuttgen *et al.*, 1971).

Recent work supports the assumption that heart rate during dynamic exercise is dependent upon the specific work procedure applied (Klausen *et al.*, 1982). Six subjects performed submaximal exercise on bicycle ergometers with one leg and two legs before and after eight weeks of one-leg training with each of both legs. During submaximal one-leg exercise heart rate decreased by 11% whereas a nonsignificant decrease of only 2% was seen during two-leg exercise at the same oxygen uptake. No changes were seen in the maximal heart rates which were greatest during two-leg exercise.

It is known that partial neuromuscular blockade during dynamic (Ockwadt *et al.*, 1959; Asmussen *et al.*, 1965; Bonde-Petersen *et al.*, 1975) as well as during static (Secher *et al.*, 1982b,c)

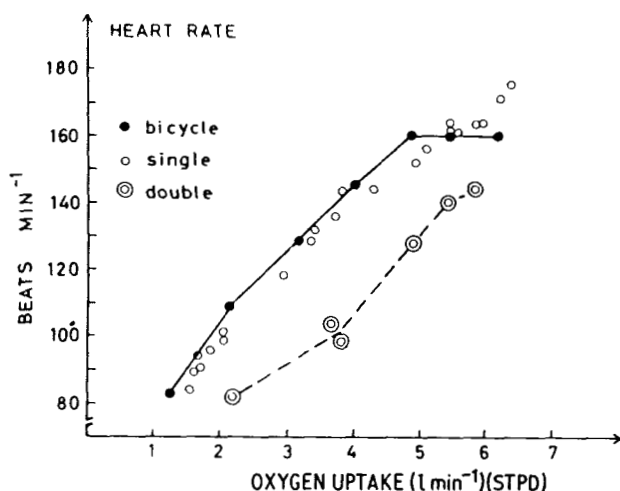


Fig. 15. Heart rate during various submaximal and maximal work loads plotted against oxygen uptake during rowing single and double sculls, and during cycling. Same subject as in Fig. 13.

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exercise increases heart rate (and blood pressure) when it is attempted to keep work intensity constant. Furthermore, during constant load static exercise, heart rate and blood pressure have been shown to vary with voluntary effort if the contraction is made easier or more difficult by vibration applied to the agonist or antagonist muscle (Goodwin *et al.*, 1972). These findings, including the measurement of heart rate during rowing, can be explained by central nervous mechanisms playing a dominant role in the regulation of cardiovascular adjustments to exercise.

Muscle characteristics in oarsmen

Human skeletal muscle consists of slow and fast twitch fibres. On average the percentage of the two fibre types in the vastus lateralis of the quadriceps and in the deltoideus muscles is generally around 50% (Johnson *et al.*, 1973; Saltin *et al.*, 1977), but the proportion of slow twitch fibres can vary among individuals from 10 to 95%. Elite oarsmen have about 70% slow twitch muscle in m. vastus lateralis as well as in m. deltoideus and only few fast twitch 'b' fibres (Bonde-Petersen *et al.*, 1975; Larsson and Forsberg, 1980; Secher *et al.*, 1981). Thus the muscles of oarsmen exhibit a fibre composition characteristic of endurance athletes (Saltin *et al.*, 1977), but with larger muscle fibre areas especially of the slow twitch fibres in m. vastus lateralis ($7300 \mu\text{m}^2$; Larsson and Forsberg, 1980) than in untrained individuals ($3600\text{--}4800 \mu\text{m}^2$; Andersen, 1975; Ingjer, 1979). The capillary network is dense in the muscles of oarsmen with values of around 600 mm^{-2} (Larsson and Forsberg, 1980) compared with around $320\text{--}350 \text{ mm}^{-2}$ in controls (Andersen, 1975; Ingjer, 1979).

It seems reasonable that oarsmen do not have many fast twitch fibres. With a cadence at racing speed of about 33 strokes per minute (Fig. 10) each stroke may have a duration of about 0.9 s. This time period allows ample time for force to be developed in the slow twitch muscle fibres, while the fast twitch fibres will have contributed only during the first part of each stroke (Warmolds and Engel, 1972; Secher *et al.*, 1978, 1981). Further, subjects with many slow twitch fibres show little muscle fatigue during repeated dynamic (isokinetic) muscle contractions (Thorstensson, 1976). This may explain why endurance athletes are found among people with many slow twitch fibres. It has been shown that people with a dominance of fast twitch muscle fibre tend to drop out of endurance training programmes (Ingjer and Dahl, 1979).

Muscle strength in oarsmen

At racing speed, Ishiko (1968) measured the force applied to the oar. In the best oarsmen the peak force varied between 700 and 900 N. Smaller values have also been reported but in less qualified oarsmen (Schneider *et al.*, 1978; Asami *et al.*, 1978).

Muscle strength is most often expressed by values recorded during maximal voluntary (isometric) muscle contractions (e.g. Asmussen *et al.*, 1959; Asmussen and Heebøll-Nielsen, 1961). The maximal forces developed during dynamic contractions become progressively smaller with increasing shortening velocity of the muscles involved as expressed by the force-velocity relationship (Hill, 1938; Wilkie, 1950).

In the force-velocity relationship the maximal power, being force times velocity, is developed at a force corresponding to about 35% of the maximal isometric force. In order to develop a dynamic rowing strength of about 800 N, it may be argued that oarsmen need an isometric rowing strength of about 2250 N.

Muscle strength of oarsmen has been measured in hand, trunk and leg muscles. The measurements do not in general separate good from less qualified oarsmen (Hagerman *et al.*, 1972; Larsson and Forsberg, 1980) although oarsmen are stronger than (Danish) controls (Table 5). Secher (1975) found that only the isometric strength measured in a simulated rowing position separates elite (2000 N) from (lighter) national and club oarsmen (1800 and 1600 N).

Table 5. Maximal voluntary strength in elite oarsmen, and in Danish controls of similar age and height.

Strength	Elite oarsmen (N)	Per cent of expected value ^a
One-leg extension	4022	118
Two-leg extension	8339	135
Backward extension of trunk	1099	115
Forward flexion of trunk	942	134
Arm strength, pull	638	118
Hand grip	746	<u>114</u>
		122

^a Asmussen and Heebøll-Nielsen (1961).

Yamakawa and Ishiko (1966) found a correlation between strength measures and rowing performance. This finding could not be confirmed by Bloomfield and Roberts (1972) and may reflect the larger body dimensions of the more successful oarsmen studied by Yamakawa and Ishiko, strength being expected to increase in proportion to p^2 (see Åstrand and Rodahl, 1977). In the 40 oarsmen studied by Secher (1975), strength measured in a simulated rowing position showed a positive correlation to hand grip strength only.

During the strength measurements it was noted (Secher, 1975) that when oarsmen extend both legs simultaneously they can develop a strength similar to or exceeding the sum of the strength measured in each of the two legs. In untrained subjects the strength of two legs is about 13–25% less than would be expected from the strength measured in each leg (Secher *et al.*, 1976, 1978). The oarsmen seem to have learned to develop an 'extra' strength when using both legs simultaneously. This finding may reflect that during, for example, walking, running, jumping and bicycling, the legs are used alternately while during rowing the legs are used simultaneously in the kick against the stretcher.

To see if the 'difference' in strength seen during one-leg and two-leg extension is dependent on muscle fibre involvement the two measures of leg strength were performed during partial neuromuscular blockade (Secher *et al.*, 1978). Two drugs were used. Decamethonium which first blocks fast twitch muscle fibres (Paton and Zaimes, 1951; Zaimes, 1953; Jewell and Zaimes, 1954) causing the contractions to be slow and enduring (Secher *et al.*, 1978, 1981). In contrast,

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tubocurarine mainly blocks slow twitch fibres (Secher *et al.*, 1982d) and the contractions are probably therefore relatively fast, and peak force cannot be sustained for more than a few tenths of a second (Secher *et al.*, 1978, 1981). Thus when decamethonium is used it is probable that the contractions are dominated by slow twitch fibres, whereas they are probably dominated by fast twitch fibres when tubocurarine is applied. During neuromuscular blockade caused by decamethonium the force developed by both legs underwent a greater fractional reduction than the force developed by one leg (Fig. 16), while the relative two-leg strength was unaffected or

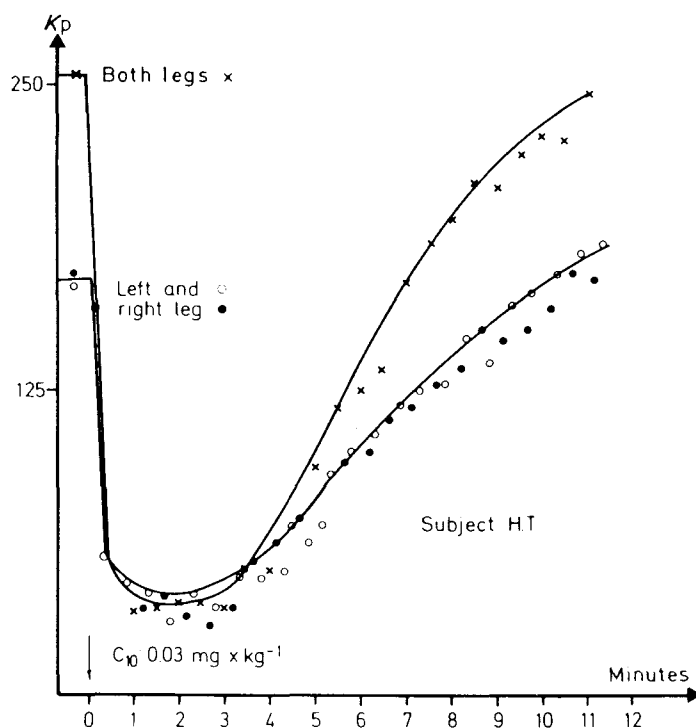


Fig. 16. Force maxima from recordings of maximal voluntary contractions before and after a single intravenous injection of decamethonium. At maximum action of the drug, strength is probably developed by slow twitch fibres. At this time two-leg strength is less than the strength developed with one leg only.

even tended to increase when tubocurarine was used. These findings may suggest that untrained individuals are unable to use the slow twitch muscle fibres as much during maximal two-leg exercise as during maximal one-leg exercise. In contrast trained oarsmen may have learned to mobilize their slow twitch fibres just as much during maximal two-leg extension as during maximal one-leg extension.

Maximal oxygen uptake in oarsmen

An increase in the total aerobic metabolism during maximal exercise of 4 to 6 min duration will be reflected by a similar increase in the maximal oxygen uptake (aerobic power, $\dot{V}O_2 \text{ max}$) of the subject (Secher *et al.*, 1982a). Thus the use of aerobic power for the assessment of aerobic metabolic capacity seems justified in oarsmen.

Maximal aerobic power measured in young untrained Swedish men is about 3.4 l min^{-1} (Bergh, 1977). In oarsmen it ranges between 2.3 l min^{-1} (Strydom *et al.*, 1967) and 6.6 l min^{-1} (Hagerman *et al.*, 1978). A direct relationship between placing x in an international championship regatta and the average maximal oxygen uptake of a crew y has been established, $y = 6.15 - 0.08x$, $r = 0.87$, $n = 10$ (Secher *et al.*, 1982e) giving a value of 6.1 l min^{-1} for first place and 5.1 l min^{-1} for 13th place (Fig. 17) when 15 to 20 crews are competing as in FISA

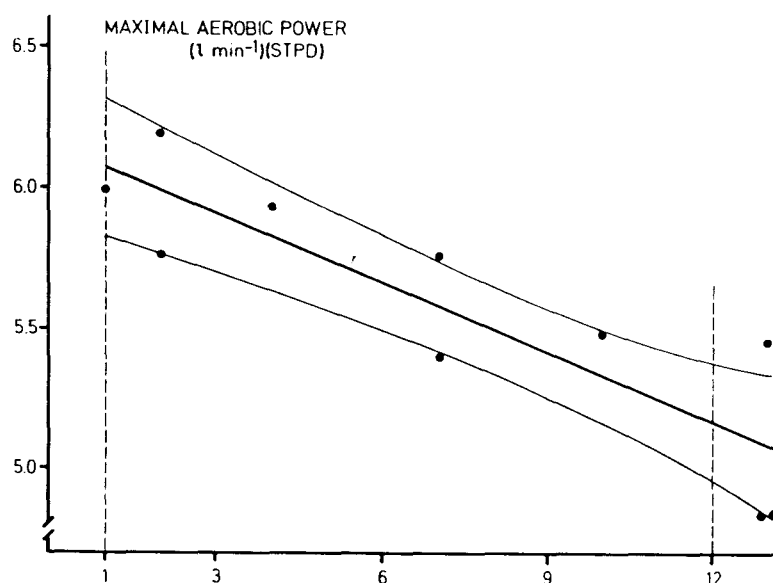


Fig. 17. Regression line between average maximal oxygen uptake of a crew and its placing in an international championship regatta.

championships. These findings indicate that the maximal aerobic power of the best oarsmen is somewhat less ($0.3\text{--}0.5 \text{ l min}^{-1}$, Tables 3 and 4) than the estimated metabolic cost of rowing at racing speed (6.38 l min^{-1}).

One group reported a maximal oxygen uptake of 7.77 l min^{-1} (Nowacki *et al.*, 1969, 1971). However, their oxygen uptake increased upwards curvilinearly with increasing work intensity. Further, the work applied on the bicycle to obtain this value was 450 W which should elicit an oxygen uptake of about 6.6 l min^{-1} only when using an efficiency value of 20% for the calculation. Another puzzling finding is a larger average maximal oxygen uptake (5.57 l min^{-1})

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at 2040 m altitude (Silvetta, Austria) than at sea level (5.09 l min^{-1}) (Ratzburg, West Germany). Both findings are explainable if the authors' apparatus overestimated large ventilations.

The large maximal oxygen uptakes of oarsmen are due mainly to their large body dimensions. When the maximal oxygen uptake is expressed per kg body weight or related to body weight to the power $2/3$ (Vaage and Hermansen, 1977), the smaller and less successful oarsmen show similar or slightly larger values (Table 3).

In Table 3 oarsmen show an oxygen uptake of about $290 \text{ ml min}^{-1} \text{ kg}^{-2/3}$, while much larger values are seen in, for example, long distance skiers (Vaage and Hermansen, 1977; Bergh, 1977). In a Danish professional bicyclist a value of $366 \text{ ml min}^{-1} \text{ kg}^{-2/3}$ can be calculated (Mikkelsen, 1980). Such a value would indicate that oarsmen with a weight of 93 kg should be able to develop oxygen uptakes of about 7.5 l min^{-1} .

A correlation between rowing performance and vital capacity (Yamakawa and Ishiko, 1966) may reflect the advantage of the larger oarsman (Equation 7), vital capacity being a volume (p^3). International competitive oarsmen have vital capacities of about 6.8 l (BTPS) with a largest recorded value of 9.1 l, but are characterized by their large aerobic power, rather than by their large vital capacity (Fig. 18).†

Hagerman *et al.* (1979) reported maximal oxygen uptakes of 4.1 l min^{-1} in women with a body weight of 68 kg, and 5.1 l min^{-1} in lightweight oarsmen. The corresponding values for

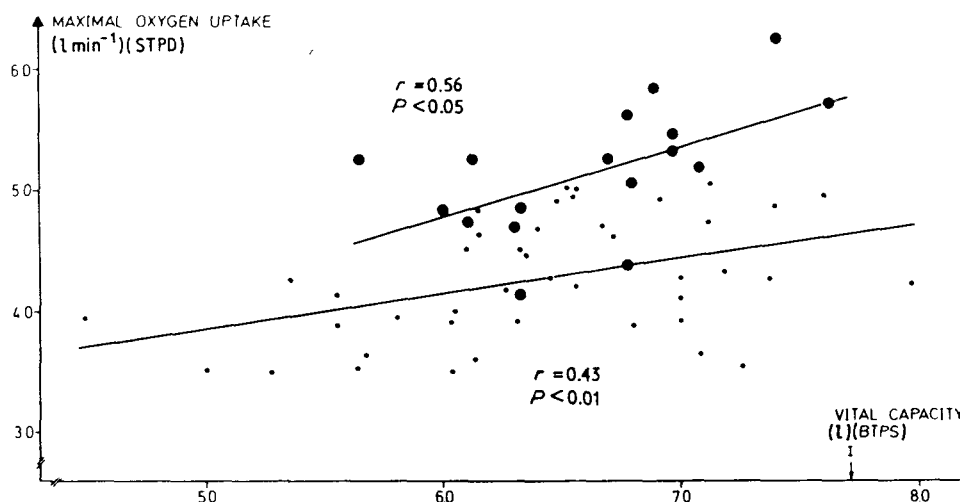


Fig. 18. Regression lines between maximal oxygen uptake ($\dot{V}\text{O}_2 \text{ max}$) and vital capacity (VC) in experienced (●) and inexperienced (○) oarsmen. Ratio $\dot{V}\text{O}_2 \text{ max} \times \text{VC}^{-1}$ 0.77 (range 0.63–0.93) in the experienced, versus 0.67 (0.49–0.80) in the inexperienced ($P < 0.001$).

† Unpublished work carried out with Roger C. Jackson, University of Calgary, Alberta, Canada. Some of these results have been presented in another form by Jackson and Secher (1976) and Åstrand and Rodahl (1977).

Danish female rowers are 3.8 l min^{-1} and 66 kg (Secher *et al.*, 1982a), while untrained Swedish women have values of about 2.1 l min^{-1} (Bergh, 1977).

It is interesting that training for rowing may increase the thickness of the left ventricular posterior wall of the heart to 12.6 mm compared with 9.4 mm in control samples and 11.1 mm in cross-country skiers and long-distance runners. These on the other hand increase the left ventricular end-diastolic diameter to 6.0 cm in relation to 5.3 cm in oarsmen and 5.0 cm in controls (Howald *et al.*, 1977). These findings suggest that training for rowing mainly leads to a pressure overload, while skiing and running lead to a volume overload of the heart, or that training for rowing increases heart dimension in the same direction as weight lifting (Longhurst *et al.*, 1980). This might be because of the involvement of the arms during rowing, but during combined arm and leg exercise, blood pressure is maintained at the same level as during leg exercise (Stenberg *et al.*, 1967; Secher *et al.*, 1977). A more likely explanation for a pressure load during rowing is the long duration of each stroke. However, blood pressure measurements during rowing have not been performed, and in the study of Keul *et al.* (1982) the dimensions of oarsmen's hearts fell within the group of endurance athletes, i.e. with a small left ventricular wall thickness in relation to the end-diastolic diameter. The later finding is in agreement with unpublished results by Lund on Danish experienced oarsmen. Thus further (longitudinal) studies of echocardiographic findings in oarsmen are needed.

The role of arm work in maximal oxygen uptake

It is known that skiing induces a larger maximal oxygen uptake than running (Åstrand, 1952; Andersen *et al.*, 1961; Strømme *et al.*, 1977). Also, arm cranking during running (Taylor *et al.*, 1955) or 'ski-walking' (Hermansen, 1973) elicit larger values than running. Laddermill climbing likewise gives larger values than running or bicycling (Kamon and Pandolf, 1972). In contrast, combined arm and leg exercise on bicycles is reported to induce the same maximal oxygen uptake as leg exercise alone (Åstrand and Saltin, 1961a; Stenberg *et al.*, 1967), but this result is probably a result of too small an arm work load (Gleser *et al.*, 1974; Secher *et al.*, 1974; Reybrouck *et al.*, 1975; Bergh *et al.*, 1976). A similar finding is a larger maximal oxygen uptake during combined arm and leg swimming (free style) than during swimming with the legs alone (Secher and Oddershede, 1975).

During rowing well-trained oarsmen obtain larger values than during bicycling (Jackson and Secher, 1976) or running (Strømme *et al.*, 1977) although conflicting reports have appeared (Strydom *et al.*, 1967; Carey *et al.*, 1974; Cunningham *et al.*, 1975; Larsson and Forsberg, 1980). Of special interest was the finding of an increase in maximal oxygen uptake during rowing but not during running in the course of a training period for competitive rowing (Larsson and Forsberg, 1980).

A discussion of the role of muscle mass in maximal oxygen uptake is of importance as it has been used to argue for the role of the heart on the one hand and for 'peripheral' factors on the other as limiting the oxygen uptake (Åstrand and Saltin, 1961a). Obviously some muscles, for example, respiratory, heart and stabilizing muscles, are active during both leg and combined arm and leg exercise. Therefore a 'direct' additional effect of maximal oxygen uptake measured during arm and leg exercise cannot be expected, but it may be expected that the maximal oxygen

uptake should increase in proportion to the increase in muscle mass if peripheral factors were of importance (Bergh *et al.*, 1976). It has been shown that maximal oxygen uptake during combined exercise is similar to that measured during leg exercise in arm-untrained subjects, but is larger than the leg value in arm-trained athletes (Secher *et al.*, 1974; Secher and Oddershede, 1975; Fig. 19). Thus when two muscle groups are working simultaneously, the maximal oxygen uptake increases in proportion to the state of training of the added muscle group.

Another question is to what extent circulation to one working muscle group interferes with circulation and oxygen uptake in another active muscle group. When severe arm exercise is added to ongoing leg exercise, leg blood flow and leg oxygen uptake decrease (Secher *et al.*, 1977). Leg blood flow and leg oxygen uptake also are smaller when both legs are working simultaneously than when one leg is working alone (Klausen *et al.*, 1982). In both models blood pressure is of a similar magnitude when work is performed with 'one' or several muscle groups. One explanation is that exercise with one muscle group induces a vasoconstriction in another working muscle group stressing the importance of vascular resistance for local oxygen uptake (Clausen, 1976; Secher *et al.*, 1977; Klausen *et al.*, 1982).

Thus it seems as if models involving combined exercise cannot reveal the relative role of the heart or peripheral limitations for maximal oxygen uptake. The question may however be

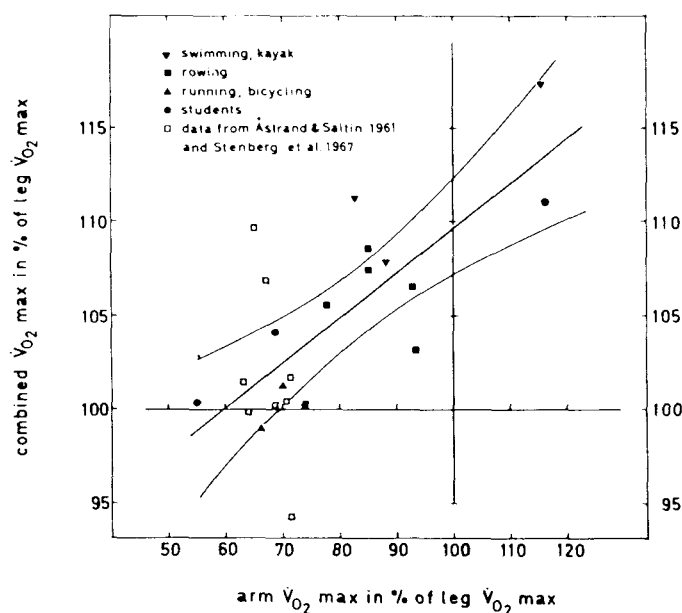


Fig. 19. Maximal oxygen uptake during combined arm and leg exercise plotted against maximal oxygen uptake during arm exercise. Both values normalized according to the subjects maximal oxygen uptake during leg exercise. Horizontal and vertical lines indicate situations where either maximal oxygen uptake during combined arm and leg exercise or arm exercise alone, are identical with the maximal oxygen uptake during leg exercise. This figure is published with the kind permission of the American Physiological Society.

academic. From a practical point of view the important question is whether peripheral factors are of significance. If peripheral factors are not of importance, all types of exercise increasing maximal oxygen uptake, for example, running or bicycling can be used for oarsmen's training. If, on the other hand peripheral factors are of importance, training for rowing should include as much rowing as possible.

It is known that endurance training increases enzyme activities, capillarization (Andersen and Henriksson, 1977; Ingjer, 1979; Klausen *et al.*, 1981) and local blood flow (Klausen *et al.*, 1982). Furthermore, it may be argued that some peripheral changes (in the arms) are needed to explain why untrained subjects have a maximal oxygen uptake during arm exercise which is about 30% less than during leg exercise, while arm-trained subjects may have a maximal aerobic power during arm exercise of up to 17% greater than during leg exercise (Secher *et al.*, 1974; Tesch *et al.*, 1974; Secher and Oddershede, 1975).

In conclusion, strength measurements as well as measurements of the metabolic and circulatory capacity in humans indicate that to a large extent training response is specific to the type of exercise trained for. If oarsmen therefore cannot row, as might happen during the winter, training sessions should be made up to simulate the work in the boat.

Acknowledgements

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References

- Andersen, K.L., Elsnér, R.E., Saltin, B. and Hermansen, L. (1961) Physical fitness in terms of maximal oxygen intake of nomadic Lapps. Technical Report, Institute of Work Physiology, Oslo, Norway.
- Andersen, P. (1975) Capillary density in skeletal muscle of man. *Acta physiologica scandinavica* **95**, 203-5.
- Andersen, P. and Henriksson, J. (1977) Capillary supply of the quadriceps femoris muscle of man: adaptive response to exercise. *Journal of Physiology* **270**, 677-91.
- Asami, T., Adachi, N., Yamamoto, K., Ikuta, K. and Takahashi, K. (1978) Biomechanical analysis of rowing skill. In *Biomechanics VI - B* (edited by E. Asmussen and K. Jørgensen), pp. 109-14. Baltimore: University Park Press.
- Asmussen, E. and Heebøll-Nielsen, K. (1955) A dimensional analysis of physical performance and growth in boys. *Journal of Applied Physiology* **7**, 593-603.
- Asmussen, E. and Heebøll-Nielsen, K. (1961) Isometric muscle strength of adult men and women. *Communications of the Danish National Association for Infantile Paralysis* **11**.
- Asmussen, E., Heebøll-Nielsen, K. and Molbech, S. (1959) Methods for evaluation of muscular strength. *Communications of the Danish National Association for Infantile Paralysis* **5a**.
- Asmussen, E. and Hemmingsen, I. (1958) Determination of maximum working capacity at different ages in work with the legs or with the arms. *Scandinavian Journal of Clinical and Laboratory Investigation* **10**, 67-71.

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- Asmussen, E., Johansen, S.H., Jørgensen, M. and Nielsen, M. (1965) On the nervous factors controlling respiration and circulation during exercise. *Acta physiologica scandinavica* **63**, 343–50.
- Asmussen, E. and Nielsen, M. (1946) Studies on the regulation of respiration in heavy work. *Acta physiologica scandinavica* **12**, 171–88.
- Asmussen, E., Secher, N.H. and Andersen, E.A. (1981) Heart rate and ventilatory frequency as dimension dependent variables. *European Journal of Applied Physiology* **46**, 379–86.
- Åstrand, P.-O. (1952) *Experimental Studies of Physical Working Capacity in Relation to Sex and Age*. Copenhagen: Munksgaard.
- Åstrand, P.-O., Ekblom, B., Messin, R., Saltin, B. and Stenberg, J. (1965) Intra-arterial blood pressure during exercise with different muscle groups. *Journal of Applied Physiology* **20**, 253–6.
- Åstrand, P.-O. and Rodahl, K. (1977) *Textbook of Work Physiology*. New York: McGraw-Hill.
- Åstrand, P.-O. and Saltin, B. (1961a) Maximal oxygen uptake and heart rate in various types of muscular activity. *Journal of Applied Physiology* **16**, 977–81.
- Åstrand, P.-O. and Saltin, B. (1961b) Oxygen uptake during the first minute of heavy muscular exercise. *Journal of Applied Physiology* **16**, 971–6.
- Balukow, C.N. (1964) Hydrodynamic characteristics of sports rowing boats. *Katera i Yachti* **3**, 187–91.
- Bergh, U. (1977) Fig. 12–5. Average maximal oxygen measure in litres per minute, millilitres per kilogram body weight times minutes per male and female Swedish national teams in different sports. In *Textbook of Work Physiology* (edited by P.-O. Åstrand and K. Rodahl), p. 408. New York: McGraw-Hill.
- Bergh, U., Kanstrup, I.-L. and Ekblom, B. (1976) Maximal oxygen uptake during exercise with various combinations of arm and leg work. *Journal of Applied Physiology* **41**, 191–6.
- Bloomfield, J. and Roberts, A.D. (1972) A correlational and trend analysis of strength and aerobic power scores in prediction of rowing performance. *Australian Journal of Sports Medicine* **4**, 25–36.
- Bonde-Petersen, F., Gollnick, P.D., Hansen, T.I., Hultén, N., Kristensen, J.H., Secher, N. and Secher, O. (1975) Glycogen depletion pattern in human muscle fiber during work under curarization (d-tubocurarine). In *Metabolic Adaptation to Prolonged Physical Exercise* (edited by H. Howald and J.R. Poortmans), pp. 422–30. Basel: Birkhauser Verlag.
- Carey, P., Stensland, M. and Hartley, L.H. (1974) Comparison of oxygen uptake during maximal work on the treadmill and the rowing ergometer. *Medicine and Science in Sports* **6**, 101–3.
- Celentano, F., Cortili, G., di Prampero, P.E. and Ceretelli, P. (1974) Mechanical aspects of rowing. *Journal of Applied Physiology* **36**, 642–7.
- Christensen, E.H. (1931) Beiträge zur Physiologie schwerer körperlicher Arbeit, *Arbeitsphysiologie* **4**, 453–69.
- Clausen, J.P. (1976) Circulatory adjustments to dynamic exercise and effect of physical training in normal subjects and patients with coronary artery disease. *Progress in Cardiovascular Diseases* **18**, 459–95.
- Cunningham, D.A., Goode, P.B. and Critz, J.B. (1975) Cardiorespiratory response to exercise on a rowing and bicycle ergometer. *Medicine and Science in Sports* **7**, 37–43.
- Furusawa, K., Hill, A.V., Long, C.N.H. and Lupton, H. (1924) Muscular exercise and oxygen requirement. *Proceedings of the Royal Society B* 167–76.
- Gleser, M.A., Hostman, D.H. and Mello, R.P. (1974) The effect on $\dot{V}O_2$ max of adding arm work to maximal leg work. *Medicine and Science in Sports* **6**, 104–7.
- Goodwin, G.M., McCloskey, D.I. and Mitchell, J.H. (1972) Cardiovascular responses to changes in central command during isometric exercise at constant muscle tension. *Journal of Physiology* **226**, 173–90.
- Hagerman, F.C., Addington, W.W. and Gaensler, E.A. (1972) A comparison of selected physiological variables among outstanding competitive oarsmen. *Journal of Sports Medicine and Physical Fitness* **12**, 12–22.

- Hagerman, F.C., Connors, M.C., Gault, J.A., Hagerman, G.R. and Palinski, W.J. (1978) Energy expenditure during simulated rowing. *Journal of Applied Physiology* **45**, 87-93.
- Hagerman, F.C., Hagerman, G.R. and Mickelson, T.C. (1979) Physiological profiles of elite rowers. *Physician and Sportsmedicine* **7**, 74-83.
- Hagerman, F.C. and Lee, W.D. (1971) Measurement of oxygen consumption, heart rate, and work output during rowing. *Medicine and Science in Sports* **3**, 155-60.
- Hagerman, F.C., McKirnan, M.D. and Pompei, J.A. (1975) Maximal oxygen consumption of conditioned and unconditioned oarsmen. *Journal of Sports Medicine and Physical Fitness* **15**, 43-8.
- Hamley, E.J. and Thomas, V. (1969) Comparison of rowing and cycling work capacity tests using heart rate as the parameter. *Journal of Physiology* **203**, 80P-81P.
- Henderson, Y. and Haggard, H.W. (1925) The maximum of human power and its fuel. *American Journal of Physiology* **72**, 264-82.
- Hermansen, L. (1973) Oxygen transport during exercise in human subjects. *Acta physiologica scandinavica* Suppl. 399.
- Hill, A.V. (1927) Muscular movement in man: the factors governing speed and recovery from fatigue. New York: McGraw-Hill. Cited in Lloyd, B.B. (1966) The energetics of running: An analysis of world records. *Advancement of Science* 515-30.
- Hill, A.V. (1938) The heat of shortening and the dynamic constants of muscle. *Proceedings of the Royal Society B* **126**, 136-95.
- Hill, A.V. and Lupton, H. (1923) Muscular exercise, lactic acid, and the supply and utilization of oxygen. *Quarterly Journal of Medicine* **16**, 135-71.
- Hirata, K.-I. (1979) *Selection of Olympic Champions*, pp. 259-305, Basel: Karger.
- Howald, H., Marie, R., Heierli, B. and Follath, F. (1977) Echokardiographische Befunde bei trainierten Sportlern. *Schweizerische medizinische Wochenschrift* **107**, 1662-6.
- Ingjer, F. (1979) Effects of endurance training on muscle fibre ATP-ase activity, capillary supply and mitochondrial content in man. *Journal of Physiology* **294**, 419-32.
- Ingjer, F. and Dahl, H.A. (1979) Dropouts from an endurance training program. *Scandinavian Journal of Sports Sciences* **1**, 20-2.
- Ishiko, T. (1968) Application of telemetry to sports activities. In *Biomechanics I*, pp. 138-46. Basel: Kruger.
- Jackson, R.C. and Secher, N.H. (1976) The aerobic demands of rowing in two olympic rowers. *Medicine and Science in Sports* **8**, 168-70.
- Jewell, P.A. and Zaimis, E. (1954) A differentiation between red and white muscles in the cat based on responses to neuromuscular blocking agents. *Journal of Physiology* **124**, 417-28.
- Johnson, M.A., Polgar, J., Weightman, D. and Appleton, D. (1973) Data on the distribution of fibre types in 36 human muscles. *Journal of the Neurological Sciences* **18**, 111-29.
- Kamon, E. and Pandolf, K.B. (1972) Maximal aerobic power during laddermill climbing, uphill running, and cycling. *Journal of Applied Physiology* **32**, 467-73.
- Keul, J., Dickhuth, H.-H., Lehman, M. and Strager, J. (1982) The athlete's heart-hemodynamics and structure. *International Journal of Sports Medicine* **3**, 33-43.
- Klausen, K., Andersen, L.B. and Pelle, I. (1981) Adaptive changes in work capacity, skeletal-muscle, capillarization and enzyme levels during training and detraining. *Acta physiologica scandinavica* **113**, 9-16.
- Klausen, K., Rasmussen, B., Clausen, J.P. and Trap-Jensen, J. (1974) Blood lactate from exercising extremities before and after arm and leg training. *American Journal of Physiology* **227**, 67-72.
- Klausen, K., Secher, N.H., Clausen, J.P., Hartling, O. and Trap-Jensen, J. (1982) Central and regional circulatory adaptations to one-leg training. *Journal of Applied Physiology* **52**, 976-83.
- Knuttgen, H.G., Bonde-Petersen, F. and Klausen, K. (1971) Oxygen uptake and heart responses to

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- exercise performed with concentric and eccentric muscle contractions. *Medicine and Science in Sports* **3**, 1-5.
- Larsson, L. and Forsberg, A. (1980) Morphological muscle characteristics in rowers. *Canadian Journal of Applied Sports Sciences* **5**, 239-44.
- Liljestrand, G. and Lindhard, J. (1920) Zur Physiologie des Ruderns. *Skandinavisches Archiv für Physiologie* **39**, 215-35.
- Linnarsson, D. (1974) Dynamics of pulmonary gas exchange and heart rate changes at start and end of exercise. *Acta physiologica scandinavica* Suppl. 415.
- Longhurst, J.C., Kelly, A.R., Gonyea, W.J. and Mitchell, J.H. (1980) Echocardiographic left ventricular masses in distance runners and weight lifters. *Journal of Applied Physiology* **48**, 154-62.
- Margaria, R., Cerretelli, P., di Prampero, P.E., Massari, C. and Torelli, G. (1963) Kinetics and mechanisms of oxygen debt contraction in man. *Journal of Applied Physiology* **18**, 371-77.
- McMahon, T.A. (1971) Rowing: a similarity analysis. *Science* **173**, 349-51.
- Mellerowicz, H. von and Hansen, G. (1965) Sauerstoffkapazität und andere spiroergometrische Maximalwerte der Ruder-Olympiasieger in Vierer mit St. vom Berliner Ruderclub. *Sportsarzt und Sportsmedizin* **16**, 188-91.
- Mikkelsen, F. (1980) *Energen Ørsted*. Copenhagen: Centrum.
- Neukirch, F. (1938) *Experimentelle Kreditslobsundersøgelser*. Copenhagen: Nyt Nordisk Forlag.
- Nigg, B.M. (1977) *Biomechanik*, pp. 178-90. Zurich: Laboratorium für Biomechanik; der ETH.
- Nowacki, P.E., Adams, K., Krause, R. and Ritter, U. (1971) Die Spiroergometrie in neuen Untersuchungssystem für den Spitzensport. *Rudersport* **26**, I-VI.
- Nowacki, P., Krause, R. and Adam, K. (1969) Maximal oxygen uptake by the rowing crew winning the Olympic gold medal 1968. *Pflügers Archiv* **312**, R66-R67.
- Ockwadt, B., Bucherl, E., Kreuzer, H. and Loeschke, H.H. (1959) Beeinflussung der Atemsteigerung bei Muskularbeit durch partiellen neuromuskulären Block (Tubocurarine). *Pflügers Archiv* **269**, 613-21.
- Paton, W.D.M. and Zaimes, E.J. (1951) The action of d-tubocurarine and of decamethonium on respiratory and other muscles in the cat. *Journal of Physiology* **112**, 311-31.
- de Pauw, D. and Vrijens, J. (1971) Untersuchungen bei Elite-Rudern in Belgien. *Sportarzt und Sportsmedizin* **22**, 176-9.
- di Prampero, P.E., Cortili, G., Celentano, F. and Cerretelli, P. (1971) Physiological aspects of rowing. *Journal of Applied Physiology* **31**, 853-7.
- Pruett, E.D.R. (1977) Fig. 16-19. In *Textbook of Work Physiology* (edited by P.-O. Åstrand and K. Rodahl). New York: McGraw-Hill.
- Reilly, T. (1981) *Sports Fitness and Sports Injuries*, pp. 155-6. London: Faber and Faber.
- Reybrouck, T., Heigenhauser, G.F. and Faulkner, J.A. (1975) Limitations to maximum oxygen uptake in arm, leg and combined arm-leg ergometry. *Journal of Applied Physiology* **38**, 774-9.
- Saltin, B. and Åstrand, P.-O. (1967) Maximal oxygen uptake in athletes. *Journal of Applied Physiology* **23**, 353-8.
- Saltin, B., Henriksson, J., Nygaard, E., Andersen, P. and Jansson, E. (1977) Fiber types and metabolic potentials of skeletal muscles in sedentary man and endurance runners. *Annals of the New York Academy of Sciences* **301**, 3-29.
- Schausen, H. (1965) Træning og kondition hos konkurrenceroere. *Tidskrift for Legemsøvelser* **30**, 29-32.
- Schneider, E. (1980) Leistungsanalyse bei Rudermannschaften. Bad Hamburg: Limpert Verlag.
- Schneider, E., Angst, F. and Brandt, J.D. (1978) Biomechanics in rowing. In *Biomechanics VI - B* (edited by E. Asmussen and K. Jørgensen), pp. 115-19. Baltimore: University Park Press.
- Secher, N.H. (1973) Development of results in international rowing championships 1893-1971. *Medicine and Science in Sports* **5**, 195-9.

- Secher, N.H. (1975) Isometric rowing strength of experienced and inexperienced oarsmen. *Medicine and Science in Sports* 7, 280-3.
- Secher, N.H., Clausen, J.P., Klausen, K., Noer, I. and Trap-Jensen, J. (1977) Central and regional circulatory effects of adding arm exercise to leg exercise. *Acta physiologica scandinavica* 100, 288-97.
- Secher, N.H., Espersen, M., Binkhorst, R.A., Andersen, P.A. and Rube, N. (1982a) Aerobic power at the onset of maximal exercise. *Scandinavian Journal of Sports Sciences* 4, 12-16.
- Secher, N.H., Mitchell, J.M., Leonard, B., Mizuno, M. and Rube, N. (1982b) Influence of central and peripheral factors on the cardiovascular responses to static contractions: Experiments with partial curarization in man. *Acta physiologica scandinavica* 114, 24A.
- Secher, N.H., Mitchell, J.M., Rube, N., Leonard, B., Mizuno, M. and Saltin, B. (1982c) Central and peripheral influence on cardiovascular responses to static contractions: Experiments with decamethonium in man. *Acta physiologica scandinavica* Suppl. 508, 44.
- Secher, N.H. and Oddershede, I. (1975) Maximal oxygen uptake rate during swimming and bicycling. In *Swimming II* (edited by J.P. Clarys and L. Lewillie), pp. 137-42. Baltimore: University Park Press.
- Secher, N.H., Rørsgaard, S. and Secher, O. (1976) Contralateral influence on recruitment of type I muscle fibres during maximum voluntary extension of the legs. *Acta physiologica scandinavica* 96, 20A-21A.
- Secher, N.H., Rørsgaard, S. and Secher, O. (1978) Contralateral influence on recruitment of curarized muscle fibres during maximal voluntary extension of the legs. *Acta physiologica scandinavica* 103, 456-62.
- Secher, N.H., Rube, N. and Molbech, S. (1981) The voluntary muscle contraction pattern in man. In *Adapted Physical Activities* (edited by J.-C. De Potter), pp. 225-36. Bruxelles: Editions de L'Université de Bruxelles.
- Secher, N.H., Rube, N. and Secher, O. (1982d) Effect of tubocurarine on human soleus and gastrocnemius muscles. *Acta anaesthesiologica scandinavica* 26, 231-4.
- Secher, N.H., Ruberg-Larsen, N., Binkhorst, R.A. and Bonde-Petersen, F. (1974) Maximal oxygen uptake during arm cranking and combined arm plus leg exercise. *Journal of Applied Physiology* 36, 515-18.
- Secher, N.H., Vaage, O. and Jackson, R.C. (1982e) Rowing performance and maximal aerobic power of oarsmen. *Scandinavian Journal of Sports Sciences* 4, 9-11.
- Secher, N.H., Vaage, O., Jensen, K. and Jackson, R.C. (1983) Maximal aerobic power in oarsmen. *European Journal of Applied Physiology* in press.
- Stenberg, J., Åstrand, P.-O., Ekblom, B., Royce, J. and Saltin, B. (1967) Hemodynamic response to work with different muscle groups, sitting and supine. *Journal of Applied Physiology* 22, 61-70.
- Strydom, N.B., Wyndham, C.H. and Greyson, J.S. (1967) A scientific approach to the selection and training of oarsmen. *Suid-Afrikaanse Geneeskundige Tydskrif vir Laboratorium en Kliniewerk* 41, 1100-2.
- Strømme, S.B., Ingjer, F. and Meen, H.D. (1977) Assessment of maximal aerobic power in specifically trained athletes. *Journal of Applied Physiology* 42, 833-7.
- Taylor, H.L., Buskirk, E. and Henschel, A. (1955) Maximal oxygen intake as an objective measure of cardiorespiratory performance. *Journal of Applied Physiology* 8, 73-80.
- Tesch, P., Piehl, K., Wilson, G. and Karlsson, J. (1974) *Kanot, Idrætsfysiologi, rapport nr. 13*. Stockholm: Trygg-Hansa.
- Thorstensson, A. (1976) Muscle strength, fibre types and enzyme activities in man. *Acta physiologica scandinavica* Suppl. 443.
- Törner, W. (1959) *Biologische Grundlagen der Leibeserziehung*, pp. 458-63. Bonn: Diemmlers Verlag.
- Vaage, O. (1977) Table 16-2. In *Textbook of Work Physiology* (edited by P.-O. Åstrand and K. Rodahl). New York: McGraw-Hill.
- Vaage, O. and Hermansen, L. (1977) Maximal oxygen uptake in a group of Norwegian top athletes trained

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- in different events. In *Textbook of Work Physiology* (edited by P.-O. Åstrand and K. Rodahl), p. 377. New York: McGraw-Hill.
- Vokac, Z., Bell, H.J., Bautz-Holter, E. and Rodahl, K. (1975) Oxygen uptake, heart rate relationship in leg and arm exercise, sitting and standing. *Journal of Applied Physiology* **39**, 54-9.
- Warmolds, J.R. and Engel, W.K. (1972) Open-biopsy electromyography. *Archives of Neurology* **27**, 512-17.
- Wilkie, D.R. (1950) The relation between force and velocity in human muscle. *Journal of Physiology* **110**, 249-80.
- Yamakawa, J. and Ishiko, T. (1966) Standardization of physical fitness test for oarsmen. In *Proceedings of the International Congress on Sports Sciences* (edited by K. Kato), pp. 435-6. Tokyo: Japanese University of Sport Sciences.
- Zaimis, E. (1953) Motor end-plate differences as a determining factor in the mode of action of neuromuscular blocking substances. *Journal of Physiology* **122**, 238-51.