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THE INFLUENCE OF TEMPERATURE ON MUSCLE VELOCITY AND SUSTAINED PERFORMANCE IN SWIMMING CARP

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Summary

The aim of this study was to evaluate how fish locomote at different muscle temperatures. Sarcomere length excursion and muscle shortening velocity, V, were determined from high-speed motion pictures of carp, *Cyprinus carpio* (11–14 cm), swimming steadily at various sustained speeds at 10, 15 and 20°C. In the middle and posterior regions of the carp, sarcomeres of the lateral red muscle underwent cyclical excursions of 0.31 μm, centred around the resting length of 2.06 μm (i.e. from 1.91 to 2.22 μm). The amplitudes of the sarcomere length excursions were essentially independent of swimming speed and temperature. As tail-beat frequency increased linearly with swimming speed regardless of temperature, the sarcomeres underwent the same length changes in a shorter time. Thus, V increased in a linear and temperature-independent manner with swimming speed. Neither temperature nor swimming speed had an influence on tail-beat amplitude or tail height.

Our findings indicate that muscle fibres are used only over a narrow, temperature-independent range of V/V_{max} (0.17–0.36) where power and efficiency are maximal. Carp start to recruit their white muscles at swimming speeds where the red muscle V/V_{max} becomes too high (and thus power output declines). When the V/V_{max} of the active muscle falls too low during steady swimming, carp switch to 'burst-and-coast' swimming, apparently to keep V/V_{max} high. Because V_{max} (maximum velocity of shortening) of carp red muscle has a Q_{10} of 1.63, the transition speeds between swimming styles are lower at lower temperatures. Thus, carp recruit their white anaerobic muscle at a lower swimming speed at lower temperatures (verified by electromyography), resulting in a lower maximum sustainable swimming speed. The present findings also indicate that, to generate the same total force and power to swim at a given speed,

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carp at 10°C must recruit about 50 % greater fibre cross-sectional area than they do at 20°C.

Introduction

Temperature has a strong influence on the contractile properties of muscles: for instance, the maximum velocity of shortening (V_{max}) of vertebrate skeletal muscle has a Q_{10} value of approximately 1.5–3.0 (Bennett, 1984). Most ectothermal animals are subjected to considerable acute, diurnal and seasonal changes in body temperature, and it would appear from the thermal sensitivity of their muscle V_{max} that they would be faced with significant problems when trying to locomote at different temperatures.

Despite changes in the contractile properties of their muscles, ectotherms are able to locomote over a wide range of temperatures. Further, the thermal dependence of the contractile properties seems to have no apparent effect on the kinematics of animals locomoting over a moderate range of sustainable speeds (Rome, 1982; Rome *et al.* 1984).

To locomote at a given speed the muscle must generate the same force and mechanical power irrespective of temperature. Owing to the change in V_{max}, cold muscle is unable to generate as much force and power per active cross-section as warm muscle. Based on electromyographic experiments on carp, Rome and colleagues (Rome *et al.* 1984, 1985; Rome, 1986, 1990) hypothesized that to generate the same force and power the animal must recruit more aerobic red fibres at lower temperatures. According to this 'compression of the recruitment order' theory, motor units are recruited in the same order at all temperatures but, to compensate for their reduced power output, the motor units are recruited over a lower range of speeds at lower temperatures. Recruiting all of their aerobic fibres (and hence having to recruit their anaerobic fibres) at a lower speed, however, results in reduced sustainable performance.

In a previous study, Rome *et al.* (1988) observed that important functional parameters of muscle (force production, power production and efficiency) at a given temperature depend on V/V_{max}, where V is the velocity at which the fibres shorten. In this paper, we measure the influence of temperature on V of the lateral red muscle at various swimming speeds in carp. Rome and Sosnicki (1990) previously determined the influence of temperature on V_{max} of carp red muscle. Thus, with values for V/V_{max} during swimming at different temperatures we can gain further insight into the problems faced and the solutions taken by ectotherms locomoting with different muscle temperatures.

Materials and methods

Animals

Carp (*Cyprinus carpio* L.) were purchased from a commercial fishery and kept in a tank at a water temperature of 15 °C for 6 weeks prior to these experiments.

The fish (11–14 cm in length) were fed daily *ad libitum* and kept on a 14 h:10 h light:dark cycle.

Measurement of sarcomere length during swimming

Our goal was to measure the sarcomere length changes with time that red muscle undergoes during swimming. The methods used for these procedures are carefully described elsewhere (L. C. Rome and A. A. Sosnicki, in preparation). Briefly, sarcomere length (SL) of the red muscle can be described by the following equations:

$$SL_{convex} = 2.06 + 1.53A/R$$

$$SL_{concave} = 2.06 - 1.53A/R \ (r^2 = 0.98),$$

where R is the radius of curvature at the backbone, and A is the half-thickness of the fish. This relationship was derived empirically by killing fish, bending them into shapes obtained during swimming, allowing them to go into rigor, and then measuring sarcomere length as a function of A/R in frozen sections. Note that in a straight fish, R is infinite, and thus sarcomere length is 2.06 μm.

Having established this relationship, sarcomere length of the lateral red muscle was calculated from the changes of curvature of fishes' bodies during the tail-beat cycle. This involved digitizing the outline of the fish and determining A/R, as in Rome *et al.* (1988).

Carp were filmed from above in a recirculating water treadmill. The water treadmill consisted of a variable-drive motor, centrifugal pump, plastic pipe sections and an acrylic swim tube (diameter 16 cm). The temperature of the unit was controlled to within 1 °C, and the fish were confined to the swim tube with upstream and downstream honeycomb grids. The flow velocity and velocity profile of the water treadmill were measured with a Swoffer water velocity meter. Although velocity dropped by about 5 cm s^{-1} within 3 cm of the walls of the swim tube, velocity in the central 10 cm of the section was quite uniform and steady with time.

Four carp were filmed (200 frames s^{-1}) from above swimming at speeds ranging from 15 to 45 cm s^{-1} with a high-speed motion picture camera (LOCAM, Redlake Corp.). To obtain a sharp silhouette of the fish in very low light levels, the bottom of the swim tube was covered with reflector material (580-10 Scotchlite, as in Wardle, 1975) and illuminated with a ring light mounted on the camera lens. Rome *et al.* (1984, 1985) found that carp avoid bright lights and prefer to swim in areas of darkness. Thus, low light levels were used and the sides and back of the swim tube were illuminated with narrow-beam high-intensity lights to prevent the fish from drifting back or taking advantage of decreased flow rates near the walls. These precautions, and the fact that the fish were too large to benefit much from the reduced flow rate near the walls of the flume, ensured that they were swimming against the full force of the water current.

Following the first series of swims at 15 °C (see Rome *et al.* 1988), fish swam at 10

and 20°C, with at least 48 h between bouts of exercise. Animals were held at the new swimming temperature for 24 h before filming. Fish were placed in the swim tube and allowed to adjust for at least 15 min with the water circulating at a moderate speed (about 15 cm s^{-1}) prior to experimentation.

The criteria for steady swimming at a certain speed were that the fish should be swimming steadily in the middle of the flume with minimal acceleration or deceleration for at least five complete tail-beat cycles. Usually three tail-beat cycles were analyzed (see Fig. 2). At slow speeds (15–25 cm s^{-1}) sufficient resolution was achieved by analyzing every fourth or fifth frame of a sequence, whereas at higher speeds it was necessary to analyze every third or second frame. Thus, depending on swimming speed, each sequence contained 40–60 frames.

Sarcomere lengths on the concave and convex sides were calculated for three positions along the length of the fish: 38 %, 52 % and 68 % of the overall length, and labelled anterior, middle and posterior, respectively. The plots of sarcomere length against time appeared to be best described as triangular waves. The velocity of shortening of the muscle was estimated for the three positions on the fish at each swimming speed using a five-point smoothing and differentiation scheme (Lanczos, 1956). The highest velocities were obtained in the rising and falling parts of the waves, and the lowest velocities at the crests and troughs, where the slope was changing sign. Sufficiently small frame intervals at each swimming speed were chosen so that the five-point smoothing and differentiation scheme gave accurate values for the maximal velocity (i.e. the endpoints did not lie in the crests and troughs of the graph). Because the rising part of the curve represented shortening of sarcomeres on the right side of the fish and the falling part of the curve represented shortening of the sarcomeres on the left side, the maximum slopes on the rising and falling portions of the curve were taken as shortening velocities. V was thus calculated as the average of the five or six maximal velocities obtained from three tail beats in each sequence.

The contribution of the tendons in the red muscle to the overall length change was considered to be negligible. In fish, the red muscle fibres are attached end to end through short myosepta. These myosepta are thin and their length change would not represent an appreciable percentage of the total change in length of the muscle–tendon complex.

Measurement of tail-beat amplitude and tail height

For each of the sequences used to determine V, the amplitude of the tail beat was also measured. Generally, at least 10 tail-beat cycles were examined and excursions averaged.

In addition, the fish were filmed from the side at each speed to look at fluctuations in tail height during swimming. A Bolex motion picture camera (framing rate 64 s^{-1}) was placed 1 m from the swim tube using the reflector material (580-10 Scotchlite) as a backdrop. With the fish swimming steadily in the middle of the tube, the error due to parallax was about 5 %, and the measurements were adjusted accordingly. We found the same rhythmical fluctuations in height as

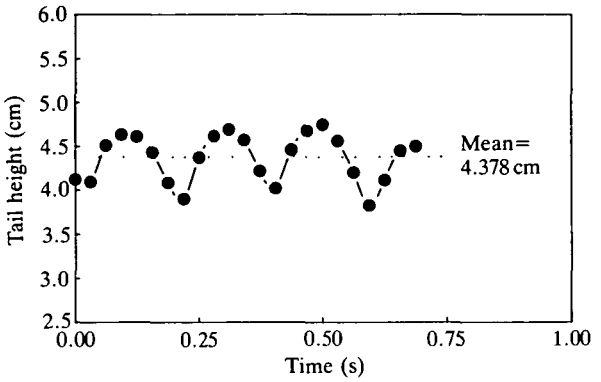

Fig. 1. Representative record of fluctuating tail height during two tail-beat cycles in a carp swimming at 20 cm s^{-1}. Measurements were taken at the trailing edge of the tail, and mean values were used to test the influence of swimming speed and temperature on tail height.

Bainbridge (1963), and used an average value calculated over about 8–10 tail beats (Fig. 1).

Electromyography

The swimming speed at which white muscle recruitment occurred was determined at each temperature by monitoring the activity of the white muscle by electromyography (see Rome *et al.* 1984, 1985). Electrodes were implanted in the white muscle on both sides of the fish with a hypodermic needle (the activity of red muscle has been previously studied in considerable detail; Rome *et al.* 1984, 1985). During this procedure fish were held in a surgical rack and anaesthetized by perfusing their gills with 50 mg l^{-1} tricaine (MS222). The electrodes were attached to high-impedance probes. Signals from the muscle were passed through a.c. preamplifiers (Grass no. P511), and recorded on two audio tracks (Cannon) of simultaneous video tape of the fish swimming during the electromyography experiments. The time and swimming speed were placed on the tape with a time–date generator (Panasonic) and video typewriter (Fora VT-100).

We found that the electrodes picked up electrical spikes from the motor of the swimming machine. Electrical interference was eliminated by building a Faraday cage around the swimming tube and enclosing the high-impedance probes within it. Typically, there was only 10–20 μV of noise.

The flow velocity was increased in steps of 5 cm s^{-1} (smaller increments of 2.5 cm s^{-1} were used near the recruitment speed), and the recruitment speed was taken to be halfway between the lowest speed at which the fish was unable to maintain position without regularly using its white muscle and the speed immediately below it.

Recruitment speeds at all three temperatures were determined in the same

animals subsequent to the filming. Recruitment speeds at 10 and 20°C were additionally determined on carp that were not filmed.

Results

Influence of temperature on sarcomere length excursion and velocity of shortening

Sarcomere length during swimming was determined from the curvature of the fishes' backbone in the films. Fig. 2 shows a typical record of the changes in sarcomere length at three places along the body of a fish swimming at 25 and at 40 cm s^{-1}.

In general, the anterior position was noisier than the middle and posterior positions. This is because curvatures were smaller in that position, and random errors (e.g. due to tracing the side of the fish with a cursor) are more apparent. In addition, the pelvic fins sometimes interrupted the profile of the side of the fish and we had to make an approximation by drawing through them. This noise made it difficult to pick out the waveform of sarcomere length with time (see especially the first half of the trace in Fig. 2B). It was thus not possible to measure accurately the amplitude (sarcomere length excursion) of the anterior waveform or its slope (muscle shortening velocity). As swimming speed and sarcomere length excursion increased, the signal-to-noise ratio in the anterior position improved, as can be seen at 40 cm s^{-1} (Fig. 2C).

We were able to film some of the fish swimming steadily at speeds ranging from 15–30, 20–40 and 20–45 cm s^{-1} at 10, 15 and 20°C, respectively (some carp could swim to only 5 cm s^{-1} below the maximal speeds quoted above; also 15°C values are recalculated from Rome *et al.* 1988). The maximum speeds at which the carp were able to swim steadily at each temperature correlated well with the initial speeds of white muscle recruitment determined by electromyography (27.1 cm s^{-1} ±S.E.=1.8, N=8 at 10°C, 36.3 cm s^{-1} ±S.E.=1.4, N=8 at 15°C and 42.9 cm s^{-1} ±S.E.=3.5, N=5 at 20°C). Thus, at the swimming speeds we filmed, the carp were using their red muscle fibres exclusively.

At higher speeds at each temperature the white muscle was recruited and the fish switched to a burst-and-coast mode of swimming. At swimming speeds below the minimum for steady swimming, the fish also used the burst-and-coast mode of swimming, but this involved recruitment of the red muscle exclusively. For instance, the fish would not swim steadily at 15 cm s^{-1} at 15 or 20°C, whereas they did so at 10°C.

Fig. 3 shows sarcomere length excursion in the middle and posterior positions at all three experimental temperatures over the range of speeds at which the fish swam steadily. Excursions ranged from 0.21 to 0.31 μm, centred around the sarcomere length in a straight fish of 2.06 μm. In these positions the excursions were essentially independent of swimming speed and temperature. The excursions in the anterior position were undoubtedly smaller (i.e. making them unanalyzable) than those in the middle and posterior positions at low swimming speeds, but they

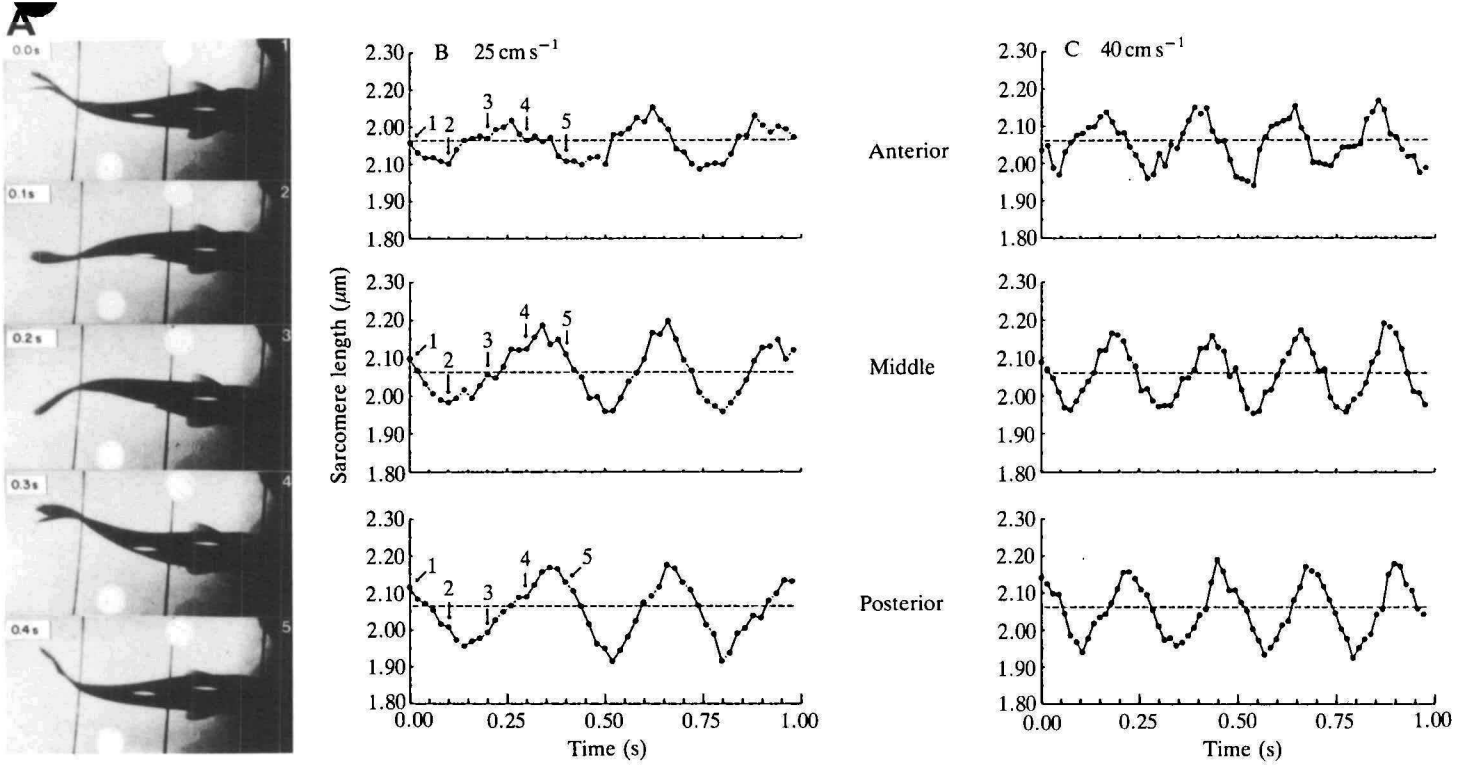

Fig. 2. Typical record showing changes in sarcomere length in anterior, middle and posterior positions of a fish swimming at 25 and 40 cm s^{-1}. Five frames (A) separated by 0.1 s are shown and numbers on the photographs correspond to data points in the 25 cm s^{-1} graphs (B). For comparison, the corresponding sarcomere length–time graph is shown for the same fish swimming at 40 cm s^{-1} (C). Note the reduction in noise and increased sarcomere length excursion in the anterior sections of the fish at the higher speed. Sarcomere length excursion (average difference between shortest and longest lengths measured in a sequence) was calculated from the amplitude of the graph. Muscle velocity was calculated from the slope of the graph. Resting sarcomere length, shown by the dotted lines in B and C, was 2.06 μm.

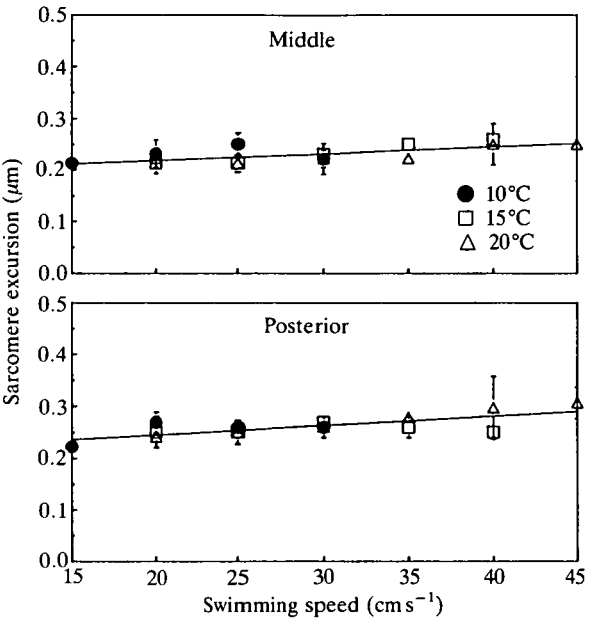

Fig. 3. Relationship between swimming speed and sarcomere length excursion at the three experimental temperatures in the middle and posterior positions on the fish. Points are means±S.E. (N=2–5). The influence of swimming speed in the middle and posterior positions was small (only at 15°C in the middle is the linear regression significant at the 0.05 confidence level). Further, temperature had no effect on sarcomere length excursion in the middle and posterior positions.

increased more significantly as the fish swam faster (i.e. the waveform became more distinct).

Tail-beat frequency was found to increase linearly with swimming speed and was independent of temperature (Fig. 4). Thus, the sarcomeres underwent the same length changes in a shorter period, resulting in an increase in muscle shortening velocity, as is shown in Fig. 5. Fig. 5 also shows that temperature had no effect on the velocity of shortening of the red muscle in the middle and posterior positions. Thus, the movements of the muscle fibres at a given swimming speed are independent of temperature.

Two parameters that influence the amount of thrust transmitted to the water are tail-beat amplitude and tail height. Fig. 6 shows that neither temperature nor swimming speed had an effect on tail-beat amplitude or tail height.

Discussion

Influence of temperature on kinematics of steady swimming and sustained performance

Over the range of steady swimming speeds, there were no changes in tail-beat amplitude or tail height with swimming speed. These results suggest that the

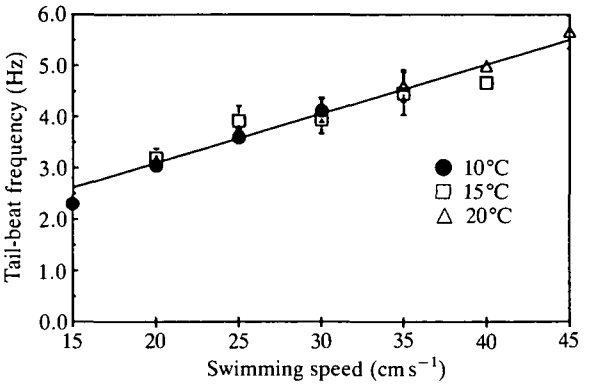

Fig. 4. Temperature had no effect on tail-beat frequency (ANCOVA, $P>0.1$). Linear increase of tail-beat frequency with swimming speed at all three temperatures is shown by the solid line (frequency=0.096×velocity+1.17, $r^2=0.98$, $N=52$). Points are means±S.E.

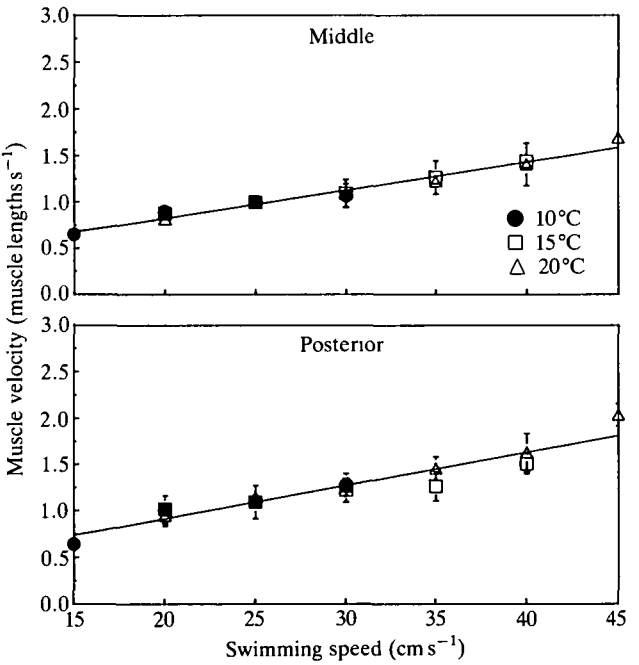

Fig. 5. Relationship between swimming speed and muscle velocity at 10, 15 and 20°C in the middle and posterior positions. Muscle velocities increase linearly with swimming speed at both positions ($r^2=0.98$ and 0.95 in the middle and posterior positions, respectively, $N=53$), due to the increase in tail-beat frequency. Temperature had no effect on velocities in the middle and posterior positions (ANCOVA, $P>0.25$ in both positions). Points are means±S.E.

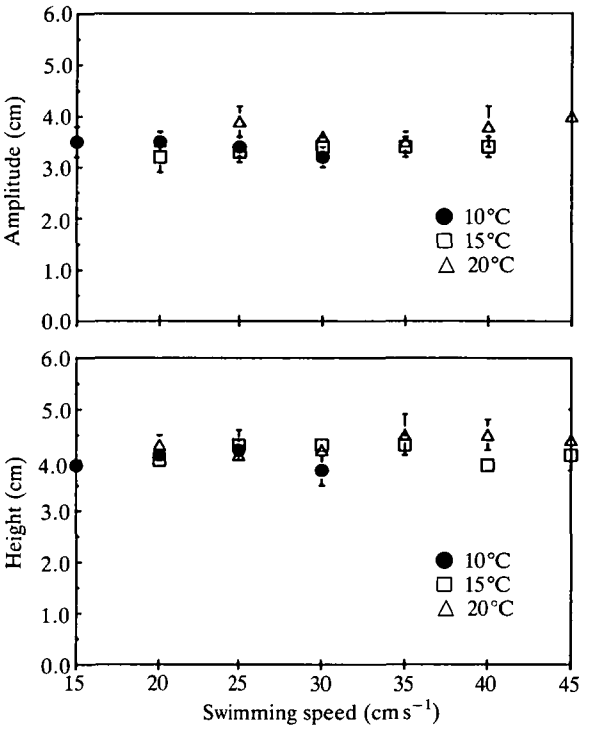

Fig. 6. Neither swimming speed nor temperature had an influence on tail-beat amplitude or tail height (ANOVA, $P>0.25$). Points are means±S.E. ($N=2$–5).

increased thrust at increasing speeds was provided solely by the linear increase in tail-beat frequency with swimming speed (in agreement with Hunter and Zweiffel, 1971). As sarcomere length excursion was independent of swimming speed, the increase in tail-beat frequency resulted in a linear increase in muscle shortening velocity with increasing swimming speed.

None of the above kinematic parameters at a given swimming speed were influenced by temperature. Previous studies of temperature effects on tail-beat frequency have shown similar temperature independence in cyprinids (Smit *et al.* 1971; Rome *et al.* 1984) and small temperature dependences in trout *Salmo gairdneri*, bass *Micropterus salmoides* (Stevens, 1979) and striped bass *Morone saxatilis* (Sisson and Sidell, 1987). The temperature independence of kinematic parameters in this study shows that, despite large changes in contractile properties, the nervous system of carp is capable of recruiting muscle so that movement at a given speed is the same at all temperatures. Similar results have been found in a very different locomotory system: lizards *Varanus exanthematicus* running at different muscle temperatures (Rome, 1982). These results suggest that there is an optimal way for an animal to locomote in a particular medium, and that this depends on anatomical parameters (e.g. origin and insertion of fibres) and the

physical properties of the environment, which are nearly independent of temperature [except for the small increase (10%) in drag of water at low temperatures].

The mechanism by which animals produce the same movements with the reduced power output of cold muscle has been termed 'compression of the recruitment order' (Rome *et al.* 1984, 1985; Rome, 1986, 1990). Motor units are recruited in the same order at low and high temperatures (red muscle motor units at low speeds followed by white ones at high speeds), but at low temperatures the order is compressed into a reduced speed range. Thus, at a given speed, more muscle fibres are recruited at the lower temperatures, compensating for their lower relative force and power outputs. This mechanism seems far more likely than the alternative mechanism of pulse coding, whereby the cold muscle compensates by having a higher level of activation (Rome, 1990).

Because fish must recruit more muscle fibres as they swim faster at any given temperature, the carp reaches a speed (maximum sustainable speed) at which it has recruited all its aerobic fibres. To generate the additional power needed to swim faster, the white anaerobic fibres must be recruited. Recruitment of the white anaerobic muscle at lower speeds at low temperatures (as observed in this study) provides the strongest evidence for the 'compression of the recruitment order' theory. Early recruitment of white muscle at low temperatures has also been reported in other fish (striped bass; Sisson and Sidell, 1987) and in lizards *Varanus exanthematicus* (Jayne *et al.* 1988). The findings in the present study agree almost perfectly with those found in previous studies of white muscle recruitment speeds in carp ($26\,cm\,s^{-1}$ at 10°C and $46\,cm\,s^{-1}$ at 20°C; Rome *et al.* 1984). We observed in this study, as well as in previous studies, that recruitment of white muscle resulted in rapid fatigue. Thus, maximum sustainable swimming speed is reduced by about one-third at 10°C compared to 20°C.

V/V_{max}: *a determinant of locomotory behaviour of carp at different temperatures*

Like cod *Gadus morhua* (Videler, 1981) and saithe *Pollachius virens* (Videler and Weihs, 1982), carp used three distinct phases of swimming: burst-and-coast swimming powered by red muscle at relatively low swimming speeds, steady swimming powered by red muscle at moderate speeds (discussed above) and burst-and-coast swimming powered by red and white muscle at high swimming speeds. All three phases were present at 10 and 20°C; however, the swimming speeds at which the transitions occurred between them were different at these two temperatures. Comparison of the value of V at which fibres are shortening during locomotion with the force–velocity characteristics of the fibres provides considerable insight into why these three phases occur and how the transition speeds vary with temperature.

Fig. 7 shows the average force–velocity and power–velocity characteristics of carp red muscle at 10 and 20°C based on measurements by Rome and Sosnicki (1990). The shaded region on each curve (outlined by vertical dotted lines) represents the range of shortening velocities, V, that were observed in this study during steady swimming. As the relationship between muscle shortening velocity

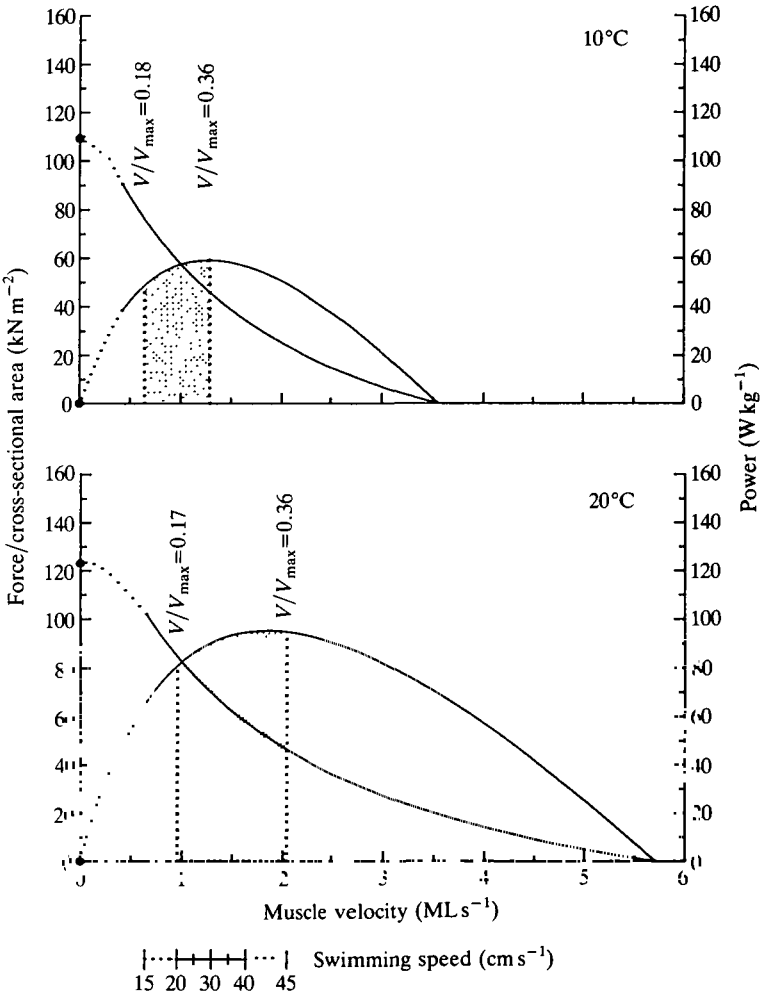

Fig. 7

and swimming speed was independent of temperature, the swimming speed axis is also shown and power, force and V of the red muscle can be related. In terms of swimming speed, the dotted vertical lines represent the transition points between steady swimming and the two phases of burst-and-coast swimming. At swimming speeds below that of the left-hand dotted line, fish burst-and-coast with red muscle. At swimming speeds above that of the right dotted line, the fish burst-and-coast with their white muscle.

Below we focus on steady swimming, followed by a brief discussion of burst-and-coast swimming at high and at low speeds.

Steady swimming

The carp swam steadily between 15 and 30 cm s^{-1} at 10°C and between 20 and 45 cm s^{-1} at 20°C. If cold fish compensate solely by recruiting more fibres, then

Fig. 7. Influence of temperature on mechanical properties of carp red muscle and on their use during swimming. This figure shows the average (see note below) force–velocity and power–velocity curves of carp red muscle at 10 and 20°C based on the results of Rome and Sosnicki (1990; the dotted portions of the curves were not covered by their experiments and are fitted by eye based on previous results). Rome and Sosnicki (1990) found that V_{max}, maximum power and maximum force generation were $3.55\,ML\,s^{-1}$, $60\,W\,kg^{-1}$ and $109\,kN\,m^{-2}$, respectively, at 10°C and $5.71\,ML\,s^{-1}$, $94\,W\,kg^{-1}$ and $123\,kN\,m^{-2}$, respectively, at 20°C, where ML is muscle length. As muscle shortening velocity during steady swimming was independent of temperature, we have placed the swimming speed axis on the graph as well (note that at 15 and $45\,cm\,s^{-1}$, the scale is shifted slightly to coincide with the actual values of V observed). Thus, during steady swimming, the curves provide the power, force and muscle shortening velocity as a function of swimming speed. The shaded regions represent the muscle shortening velocity during steady swimming with red muscle. The dotted vertical lines at each temperature represent transition swimming speeds. At slower swimming speeds than that of the left-hand line, the carp used burst-and-coast swimming with red muscle. At higher swimming speeds than that of the right-hand line, the white muscle is recruited and the carp used burst-and-coast swimming. For each temperature, the V/V_{max} at the transition points is given. In addition to the above V_{max} values, the curves were defined by the following coefficients: $a/P_o^*=0.455$ and $P_o^*=1.19$ at 10°C and $a/P_o^*=0.30$ and $P_o^*=1.29$ at 20°C, where a is the Hill constant and P_o^* is the extrapolated load at zero velocity. Note that the coefficients were chosen so that the curves above gave the best fit to important average parameters (e.g. maximum power, force at a given V). Hence they differ somewhat from the average coefficients quoted by Rome and Sosnicki (1990; a hyperbolic curve with average coefficients may be skewed and may not accurately represent the average shape).

comparing V and the force–velocity characteristics of red muscle should enable us to quantify the relative numbers of fibres recruited at each temperature. To swim steadily at a given speed, the carp's muscles must generate the same total power at both 10 and 20°C. Because V is independent of temperature, this means the muscle must generate the same total force (i.e. power=force×velocity). Fig. 7 shows that, at a swimming speed of $20\,cm\,s^{-1}$ ($V=0.95\,ML\,s^{-1}$, where ML is muscle length), the muscle would generate $60\,kN\,m^{-2}$ at 10°C and $85\,kN\,m^{-2}$ at 20°C. Thus, the fish must recruit 1.42-fold greater fibre cross-section at 10°C to generate the same total force. This ratio increases as swimming speed increases. At $30\,cm\,s^{-1}$ ($V=1.28\,ML\,s^{-1}$), the red muscle at 10°C generates $46\,kN\,m^{-2}$ and at 20°C generates $70\,kN\,m^{-2}$; thus 1.53-fold greater fibre cross-section must be recruited at 10°C than at 20°C.

Although it is clear that at 10°C the carp must recruit all its red motor units (and hence start to recruit its white ones) at a lower speed of swimming, the comparison of V and V_{max} predicts the swimming speed at which this occurs at different temperatures. Fig. 7 shows that recruitment of white muscle occurred at both temperatures at a V where red muscle power output started to decline (right-hand vertical dotted lines; $1.28\,ML\,s^{-1}$ at 10°C and $2.04\,ML\,s^{-1}$ at 20°C) in the face of the requirement of generating additional power to swim faster. The 1.6-fold higher V at 20°C than at 10°C is matched by a Q_{10} of 1.63 for V_{max} and thus the

recruitment of white muscle occurred at both temperatures when V/V_{max} of the red muscle reached a value of 0.36. Therefore, because of its lower V_{max}, cold carp must recruit its white muscle at slower swimming speeds.

Burst-and-coast swimming at high speeds with white muscle

In addition to a possible hydrodynamic advantage (Weihs, 1974; Videler and Weihs, 1982), an energetic advantage may be realized by the muscle fibres of carp during burst-and-coast swimming. Although energetics measurements were not made in this study, the efficiency of fish muscle is known to decrease from a maximal value as V/V_{max} drops below about 0.2 (Curtin and Woledge, 1988). The carp in the present experiments appear to adopt a burst-and-coast pattern of swimming when the major muscle fibre type used would have too small a V/V_{max} to generate power with a high efficiency if the fish were swimming steadily. The burst-and-coast pattern allows the fish to make the normal sarcomere excursion in a shorter time (shorter duty cycle), resulting in a higher V (and V/V_{max}).

For instance, carp used the burst-and-coast mode of swimming at high swimming speeds when the white muscle was recruited. Because of its higher V_{max} and two- to fourfold greater gear ratio (Rome *et al.* 1988; L. C. Rome and A. A. Sosnicki, in preparation), if the fish were to continue swimming steadily the white muscle would be shortening with a low V/V_{max}. Thus, the fish makes rapid tail beats with white muscle and obtains a two- to threefold higher V (G. J. Lutz and L. C. Rome, unpublished finding) and presumably a more optimal V/V_{max}.

Burst-and-coast swimming at low speed with red muscle

Carp also switch to burst-and-coast swimming at low swimming speeds (at both temperatures) where V/V_{max} in the red muscle decreased below 0.17. Because V_{max} was 39 % lower at 10 °C than at 20 °C, at 10 °C carp could use its red fibres to a 36 % lower V. Hence, at 10 °C the carp could swim steadily at 15 cm s^{-1}, whereas at 20 °C the carp used burst-and-coast swimming at speeds below 20 cm s^{-1}, possibly to maintain a relatively higher V/V_{max}.

V/V_{max}: *a design constraint of muscle*

V/V_{max} appears to set both the lowest and highest velocities over which a fibre can be effectively used during locomotion (i.e. V/V_{max}=0.17–0.36) at both low and high temperatures. Previously, Rome *et al.* (1988) showed that, at a given temperature, slow red and fast white muscle are used over a similar range of V/V_{max}, despite their 2.6-fold difference in V_{max}. In any particular fibre arrangement, it is likely that the parameters that limit the range of V over which a given muscle fibre type is used are the reduced efficiency at low V/V_{max} and the reduced power output at high V/V_{max}. Despite the large differences in V_{max} between fibre types and at different temperatures, muscles are used precisely over the same range of V/V_{max}. This suggests that V/V_{max} is an important constraint.

V/V_{max} is not the only design constraint in muscle. L. C. Rome and A. A. Sosnicki (in preparation) have shown that myofilament overlap is an important

constraint; that is, fibres are anatomically arranged so that nearly maximal overlap is maintained during all movements. In addition, the extensive work of Josephson (e.g. 1985), Marsh and Bennett (e.g. Marsh and Bennett, 1985; Marsh, 1988), and Stevens (e.g. 1988) suggests that the kinetics of activation and relaxation may be important as well. By reproducing *in vitro* the exact stimulation pattern and length changes the muscle undergoes *in vivo*, we should be able to evaluate their relative importance.

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