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ISABEL PEREZ FARFANTE

Northeast Fisheries Center Systematics Laboratory
National Marine Fisheries Service, NOAA
National Museum of Natural History
Washington, DC 20560

ON THE ROLE OF THE DIFFERENT FIBRE TYPES IN FISH MYOTOMES AT INTERMEDIATE SWIMMING SPEEDS

In most fishes the myotomal locomotor musculature is made up of two main fibre types: a superficial layer of red fibres overlies the white fibres which form the main mass of the myotome. A spectrum of such differences as mitochondrial content, enzyme activities, blood supply, and innervation (as well as color) distinguishes these two fibre types. The electrophysiological properties of the two fibre types have only been investigated in a few species, but in all of these the white fibres have been found to propagate muscle action potential, whereas only local nonpropagated activity is seen from red fibres (which are invariably multiply innervated). In many (but not all) fishes, there are also other less abundant fibre types in the myotomes, in some respects intermediate between the red and the white fibres (e.g., Patterson et al. 1975).

There is general agreement that at low sustained swimming speeds only the red fibres are employed and that the white fibres are active dur-

ing short bursts of maximum speed, which cannot be long sustained. However, agreement has not yet been reached about which fibres are active during sustained swimming at speeds above the minimum cruising speed. Indirect evidence from a number of teleost species (e.g., Greer Walker and Pull 1973) indicated that the white fibres are active at these intermediate swimming speeds, as did the direct electromyographic investigations of Hudson (1973). More recently, several workers have suggested that fibres of intermediate type are recruited as swimming speed rises from the minimal cruising speed, before white fibres are activated and the fish attains its maximal sustained speed. In this note, we report electromyographic observations on various teleosts swimming at controlled speeds in a tunnel respirometer, which show that the activity of the myotomal fibre types during sustained swimming is different in different fishes.

Material and Methods

We studied herring, carp, and trout. Juvenile Pacific herring, *Clupea harengus pallasii* Valenciennes, 15-17.5 cm FL (fork length) were caught by seining in the Georgia Straits, B.C., and held in circulating seawater at the Department of Zoology, University of British Columbia, until swum in a tunnel respirometer (Brett 1964). Herring are delicate fish and did not settle quietly in the respirometer at flow lengths below 2-3 body lengths per second (BL/s). Instead, they darted upstream and fell back again in an irregular manner, so that it was necessary to force them to swim at such speeds from their first entry to the apparatus, without the acclimation period usual when working with other fishes.

Varnished copper wire (40 standard wire gauge) electrodes bared at the tips were placed in the postanal myotomes. The fish were anaesthetized with MS-222¹ (Sandoz) and the electrodes sutured to the dorsal surface before being led downward and backward to enter the myotomes. After recovery for 30 min or so in a bucket of seawater, the fish were introduced to the respirometer and muscle potentials recorded on a Gould Brush 220 pen recorder via Tektronix 122 preamplifiers. It proved difficult to record from electrodes whose tips lay amongst the white muscle fibres, but activity from

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

these fibres was picked up by electrodes whose tips lay in the thin lateral red muscle strip. Relative proportions of red and white muscle fibres were determined by dissection, and their innervation patterns were examined in Formalin-fixed material. Cryostat sections stained for lipid and for succinic dehydrogenase by routine methods were used to distinguish different fibre types.

Similar studies were carried out on carp, *Cyprinus carpio* Linnaeus, 25-30 cm FL, caught by seining in the Fraser Valley, B.C., and rainbow trout, *Salmo gairdneri* Richardson, 17-30 cm FL obtained from a commercial supplier. Before trial in the respirometer both species were held in circular tanks around which water was pumped to give a constant flow of 30-40 cm/s around the circumference where the fish normally swam. For these freshwater fish, much improved sig-

nal : noise ratios were obtained by adding small amounts of seawater to the freshwater in the respirometer; this did not affect the behavior of the fish, which were allowed to acclimate for 18-20 h in the apparatus before testing.

Results

Pacific Herring

The records of muscle activity shown in Figure 1A-C are from electrodes with their tips lying in the lateral strip of red muscle. These records show that bursts of irregular potentials around 200-300 μV peak to peak are recorded from the red fibres during slow sustained swimming, becoming more synchronous and shorter as swimming speed increases and tail beat frequency rises. At sustained



FIGURE 1.—Records from lateral red muscle of a juvenile Pacific herring (16.4 cm fork length) swimming at different speeds. A: 1.8 body lengths per second; B: 2.8 body lengths per second; C: 3.1 body lengths per second; and D: 4.3 body lengths per second. Note gradually increasing synchrony of potentials as swimming speed and tail beat frequency rise (A-C), and the appearance of large potentials in D (picked up from underlying white fibres) when the fish struggled to maintain position at high flow speed. Vertical bar: 500 μV ; time marker: seconds.

swimming speeds up to 4-5 BL/s, these are the only kind of potentials recorded; no larger potentials are observed. Because herring are delicate fish, velocity/endurance experiments in respirometers or water tunnels are likely to underestimate their real capabilities, for it is probable that they slowly deteriorate during their sojourn under experimental conditions. Our limited series of measurements of sustained swimming speeds (Figure 2) showed that juvenile herring were able to maintain speeds around 4 BL/s for periods of at least 5 h, a performance about double that previously observed by Boyar (1961), but similar to that seen in large circular tanks by Hempel (in Blaxter 1969).

Boyar's study was very much more extensive than ours; some of his results are plotted in Figure 2 for comparison, where it can be seen that the form of the velocity/endurance curves we obtained is similar to those found for other fish (e.g., Hunter 1971). It seems probable that 4-5 BL/s represents a sensible upper value for continuous sustained cruising by herring of this size.

If the speed of flow in the respirometer is increased above this speed, or if the fish becomes progressively exhausted, it intersperses periods of steady swimming, as before, (during which it slowly falls back to the downstream electrified grid) with a few rapid tail beats, which drive it upstream, and the cycle is repeated. During these rapid beats (Figure 1D), large potentials around 1 mV are observed. Similar potentials are seen when the fish is struggling, and there can be no doubt that (as in dogfish, Bone 1966) the electrodes in the red fibre layer pick up these large potentials from the underlying white fibres. White fibres in

herring are similar to those of dogfish in that they are focally innervated (Bone 1964) and they must therefore propagate action potentials. The white fibre system in herring was rapidly exhausted, for the fish could not swim at velocities above 5 BL/s for more than 1-2 min (as indicated in Figure 2). Thus there is good accord between our electromyographic observations and the values obtained for maximum sustained swimming velocities: in herring only red muscle fibres are employed during sustained cruising.

Histologically, the red and white fibres are different from each other. The red fibres are of more or less uniform diameter, are multiply innervated, and lipid and succinic dehydrogenase (SDH) positive. In contrast, the white zone of the myotome contains both large fibres, and much smaller fibres arrayed around them in a sort of lattice. Both types contain little lipid, are SDH negative, and there are no intermediate fibres either in the juvenile herring which we examined in the respirometer, or in adults. These histological arrangements are summarized in Figure 3A.

Carp

The carp used were much more robust and larger fish than the Pacific herring and it proved possible to make simultaneous recordings of activity within white and red portions of the myotomes. The results obtained were entirely different from those seen in the herring. At speeds between 0.5 BL/s (the lowest speed at which the fish would swim reliably) and the maximum speed used, around 4 BL/s, electrical activity was always detectable from both sets of electrodes in red and white zones of the myotomes (Figure 4). As speed increases from the lowest values, the bursts of activity from each zone became more synchronous and shorter and their amplitude increased. Occasional spikes of greater amplitude were observed from the white muscle zone (Figure 4B), these were faster events than those composing the remainder of the motor bursts. When the fish was swimming near the maximum speed sustainable in the respirometer (Figure 4C), these rapid potentials formed the larger part of the motor bursts and were always seen on both red and white recordings, though smaller from the former. Presumably, they represent spikelike activity from the white zone of the myotome, picked up (as in herring) by electrodes in the red zone. Since the red and white electrodes did not lie in the same

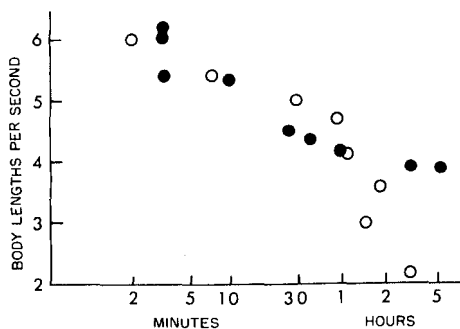


FIGURE 2.—Swimming speeds (in body lengths per second) plotted against the time that the speeds were sustainable (abscissa). Dots: present observations; open circles: data plotted for comparable fish from Boyar (1961). Note the different forms of the velocity/endurance curves given by the two sets of fish, probably the consequence of damage to Boyar's fish in his apparatus.

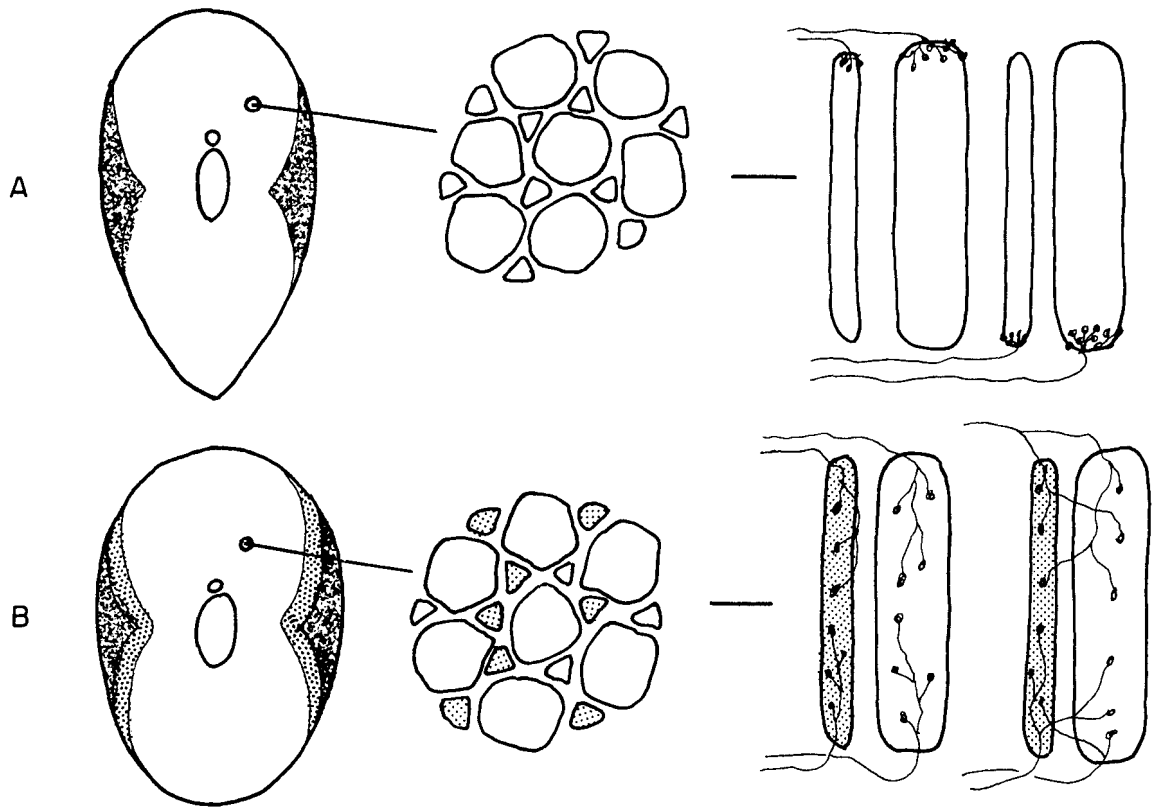


FIGURE 3.—Diagram summarizing the organization of white muscle fibres in the myotome of Pacific herring (A), compared with those of rainbow trout and carp (B). It is not known whether a single axon may supply both large and small white fibres in herring (though both are focally innervated), nor is it known which of the two alternative innervation patterns for rainbow trout and carp are actually present. An overlap of innervation between small and large fibres seems most likely. Note the presence of intermediate fibres between red and white zones of the myotome in carp and rainbow trout; they are absent in herring. (B partly after Patterson et al. 1975 and Johnston et al. 1977.)

myotome (though on the same side of the fish and fairly close to each other), the appearance of occasional spikelike potentials in the white zone was not always reflected directly in the record from the red. At lower swimming speeds, when the electrodes in the white zone did not pick up spikelike potentials at every tail beat, higher recording speed (Figure 4D) showed the variety of response from the white zone of the same myotome at successive tail beats.

Spikelike potentials were present (although usually <0.5 mV in amplitude) and were often reflected at lesser amplitude by the electrodes in the red portion of the myotome, but there were also much smaller irregular potentials from the white region of the myotome, resembling the smaller irregular potential bursts from the multiply innervated red fibres. In carp, both red and white muscle fibres are multiply innervated and there

are intermediate fibres lying between red and white fibre zones (Figure 3B). The electrodes in the white portion of the myotome were placed close to the spinal column so that they did not lie near the intermediate zone recently described by Johnston et al. (1977).

Our results clearly indicated that the white fibres were active even at low swimming speeds, and that the activity at these speeds did not resemble the spikelike muscle potentials observed when the fish are swimming faster.

Rainbow Trout

Rainbow trout were examined last of the three fish studied and, to our surprise, gave results comparable with those from the herring, although in salmonids the white fibres are multiply innervated, as they are in carp. At speeds below 2 BL/s, no activity was detectable from the white (mosaic)

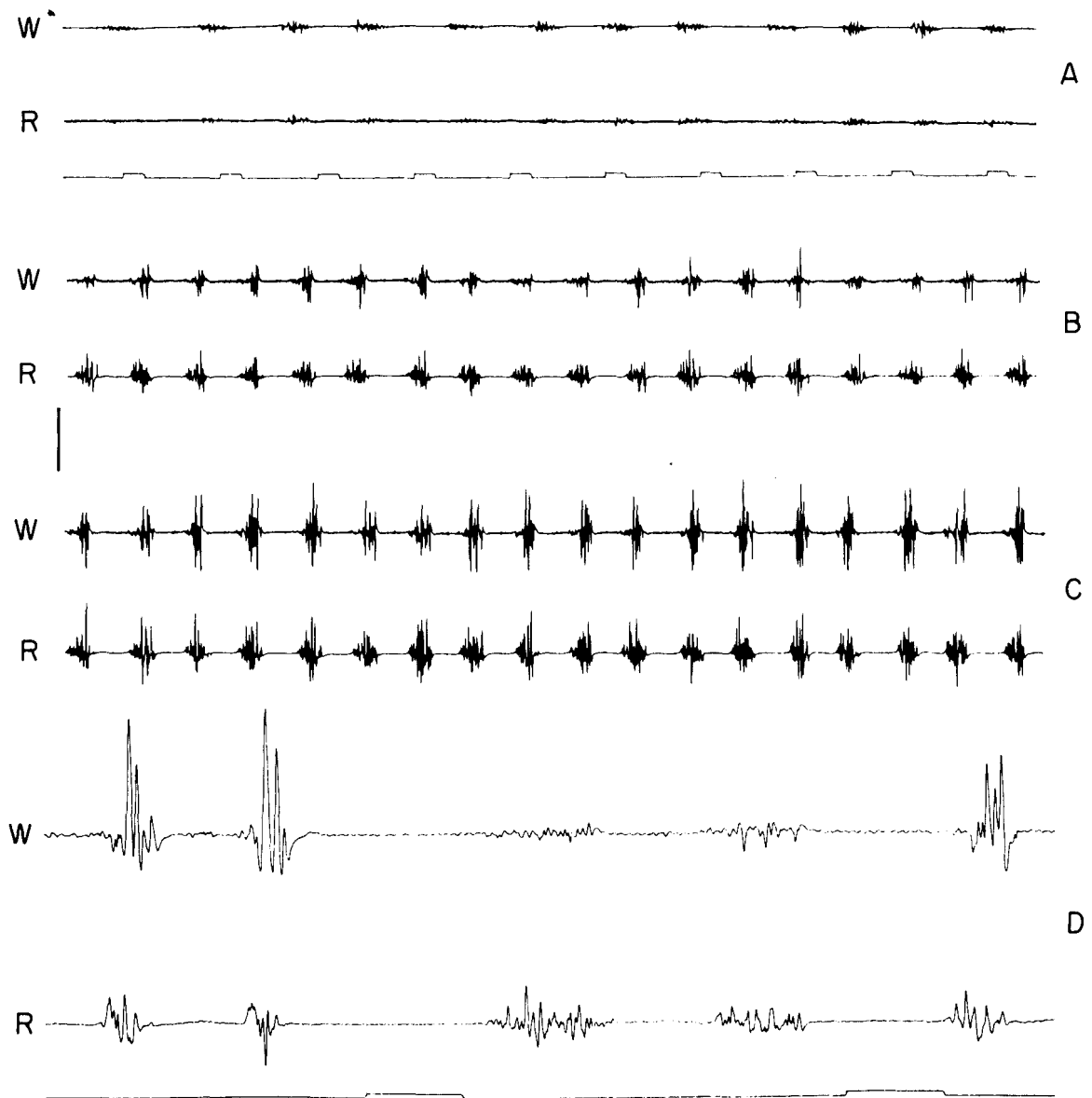


FIGURE 4.—Records of activity from red (R) and white (W) regions of a carp myotome at different swimming speeds. A: 0.75 body length per second; B: 0.9 body length per second; C: 1.26 body lengths per second; and D: 2.0 body lengths per second. Note that the white fibres are active even at low swimming speed and that there is spikelike activity at each tail beat in C. The lowest record (D) taken at higher chart speed shows the appearance of irregular bursts containing spikelike potentials. Note pick-up of these events by the overlying red fibre electrode. Vertical bar: 500 μ V; time marker: seconds.

zone of the myotome: 1-200 μ V potentials of the usual kind were obtained from the lateral red musculature (Figure 5A). When startled, a few rapid tail beats drove the fish forward and, under these conditions, larger spikelike potentials around 0.5 mV peak to peak were recorded from the white zone of the myotome corresponding to

the rapid tail beats. As can be seen from Figure 5B, these events were picked up at lower amplitude by the electrodes whose tips lay in the lateral red muscle layer. After a few rapid tail beats, the fish coasted forward before dropping back and resuming regular swimming: the normal rhythm of the red fibre system was inhibited for a few cycles.

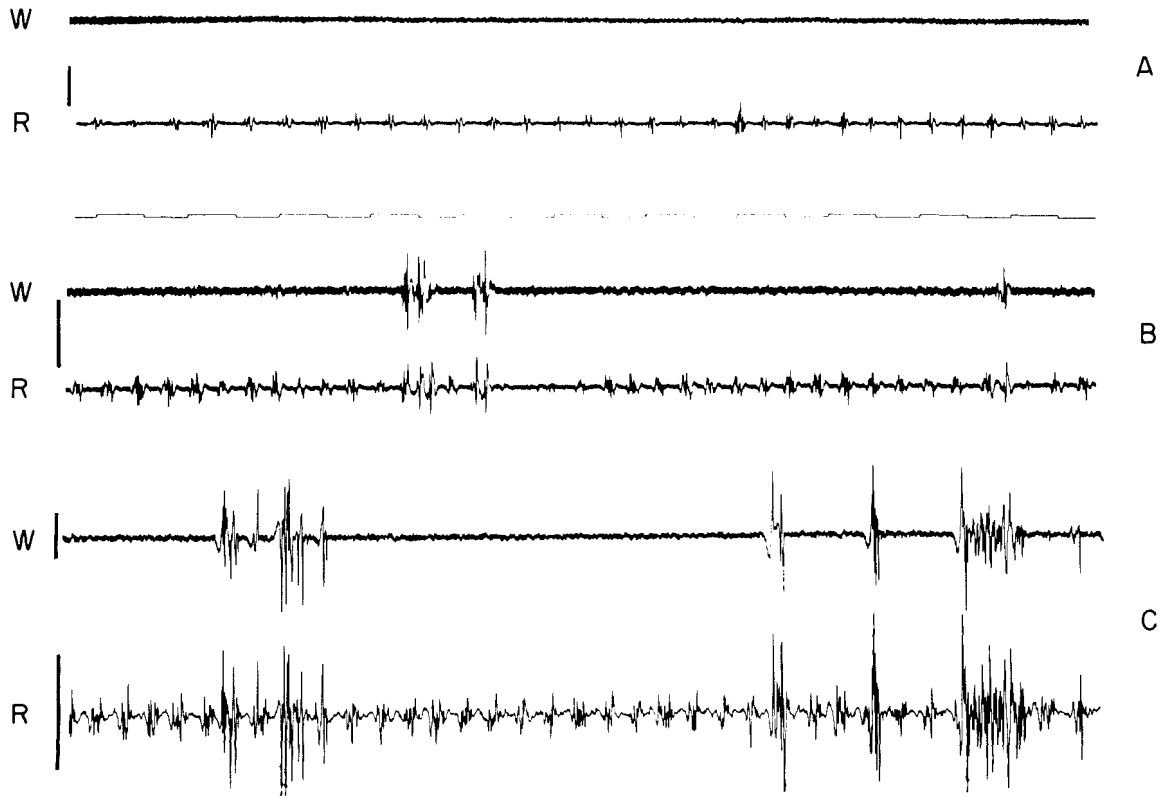


FIGURE 5.—Records of activity from red (R) and white (W) regions of the myotome of different rainbow trout swimming at various speeds. A: 1.8 body lengths per second; B: 4.6 body lengths per second; C: 2.2 body lengths per second. Note that during regular sustained swimming involving red muscle activity, no activity is detected from the white zone of the myotome. Occasional spikelike activity from the white zone of the myotome is seen in B and C (also picked up by the electrode lying in the overlying red zone of the myotome), sometimes inhibits the red muscle bursts (B) and sometimes does not (C). Vertical bars: 1 mV; time marker: seconds.

A single rapid tail beat (to the right of the record) interrupted the red muscle for a single cycle. At higher sustained speeds, above 2 BL/s (as in Figure 5C) this inhibition of red activity following single rapid movement no longer took place. Rather, the behavior was similar to that of the herring in that the fish fell gradually back despite the regular activity of the red system, until driven forward again by a few rapid beats; to drop back again and repeat the cycle until the white system was exhausted. Under these conditions, the fish did not "coast" following rapid tail movements.

No electrical activity was observed from the white zone of the myotome (the so-called mosaic zone) apart from the spikelike potentials shown in Figure 5B and C, although particular pains were taken to ensure that the electrodes were recording satisfactorily. All the fish recorded from gave this same result. We conclude from our observations that this part of the motor system is not active at

speeds below 2-2.5 BL/s. Figure 3B summarizes the structure of the system.

Discussion

Our observations have shown once again that the lateral red musculature is used by fish for sustained slow cruising, and that rapid movements of the tail are brought about by the activity of the white motor system, during which spikelike potentials can be recorded from the white zone of the myotome. At intermediate speeds, there are manifest differences between different fishes.

The simplest situation is shown by the Pacific herring, where sustained activity depends only on the activity of the red motor system of the myotome: the white fibres play no part in any activity except rapid movements of short duration. It is true that such movements can "top up," as it were, the sustained activity of the red motor sys-

tem, but this process cannot be long continued: in the respirometer flow velocities which overload the red system and involve occasional activity from the white system soon exhaust the fish. Presumably this artificial situation, where the fish are forced to swim at such speeds, is not found in nature.

The taxonomic position of clupeids is not yet agreed upon (see Greenwood et al. 1966), but in the organization of their myotomal motor system they show the primitive pattern of focal innervation of the white fibres (Bone 1970) found also in elasmobranchs, Agnatha, and dipnoi, but in few other teleosts.

We may surmise that in all fish where the white motor system is innervated in this way, sustained swimming will be the responsibility of the red system alone, as it is in herring and dogfish. It is important to notice that this is not to say that gradation may not take place separately within either system. For example, there are five fibre types in the dogfish myotome (three slow and two fast) distinguishable by histochemical and ultrastructural criteria, and it is entirely reasonable to suppose that the two fast fibre types are recruited for movements of different rapidity as Kryvi and Totland (1977) have suggested. At present, our preliminary ultrastructural and histochemical investigations of young and adult herring myotomal fibres have only shown one type of red fibre and two types of white fibre. The two white fibre types may operate at different stages during rapid swimming, but there is no direct evidence for this assumption, and it may be more reasonable to interpret the smaller white fibres as growth stages in the development of the larger (see Bone in press).

In carp, the situation during sustained swimming at all speeds is entirely different. There is inevitably some ambiguity in the interpretation of electromyographic records since the position of the electrode tip may not be certainly known, and the records obtained may be from nearby small electrical events or from distant larger ones, but it certainly does not seem probable that the small events recorded from the carp white muscle at slow sustained swimming speeds can have been picked up from the distant red muscle system. To judge from our records taken deep within the white muscle, as far as possible from the lateral red strip, some fibres within the white zone are active even at the slowest sustained speeds, and this activity increases as the fish increases its

swimming speed. This kind of electrical activity at the slower sustained speeds is very similar to that of the red motor system, and presumably represents the activity of fibres which are not propagating muscle action potentials. Such records could not, naturally, be obtained from the white system of fish where the white fibres are focally innervated, and in fact are not seen in herring or dogfish. At higher sustained speeds, or when the carp is disturbed, much larger rapid potentials are observed from the electrode within the white zone. Plainly, two alternative explanations are possible for the variety of electrical response from a single recording site within the white muscle. Either the electrode tip lies close to fibres of two different types, one of which is capable of propagating muscle spikes and the other is not. In this situation, the potentials observed simply reflect the fact that the former system is only activated at higher speeds, the latter operating during slow swimming and so resembling the red motor system. In other words, in the carp myotome, the arrangement is essentially a mosaic one, in which red fibres are intermingled with the usual fast fibres of the white zone. Or, alternatively, the white zone contains only a single muscle fibre type, which is capable of local contractions not involving muscle action potentials, but can also be stimulated to twitch rapidly and, in this state, propagates muscle action potentials. As pointed out earlier (Bone 1975) this would be an ingenious way of ensuring for a single muscle fibre that it always operated at the flattened upper part of the power curve, contracting at very different rates whilst swimming slowly and rapidly.

Our electromyographic records do not allow us to distinguish between these two alternatives but there is no evidence from the histochemical studies by Patterson et al. (1975), or the recent excellent paper by Johnston (1977), that there are "red" fibres in the white zone of the carp myotome. These authors have demonstrated clearly, however, that there is a zone of intermediate fibres between the lateral red and deep white fibres of the carp myotome. They have also shown that these three fibre types are active at different swimming speeds. At 1 BL/s only red fibres were found to be active; at 1.3-1.5 BL/s both red and pink fibres were active, whereas at 2.0 BL/s and above, electrical activity appeared from the white zone of the myotome. These results clearly indicated the sort of recruitment of intermediate fibres at intermediate sustained swimming speeds

which was implied by their accompanying biochemical studies. Interestingly enough, Johnston et al. (1977) observed the same kind of electrical activity from the white zone of the myotome that we observed at low speeds, and it seems therefore extremely probable that such activity (around 75 μ V in their records at 2.0 BL/s) is indeed generated by muscle fibres in the white zone. They did not observe spikelike activity from the white zone, presumably because their fish were not swimming sufficiently fast, i.e., they investigated only the lower sustained swimming speed range.

It is then still an open question whether individual fibres in the white zone can sometimes operate producing only local potentials, at other times generating muscle action potentials; or whether there are two different fibre types in the white zone, as yet not distinguishable histochemically. We incline to the former opinion, but to settle the matter evidence from intracellular studies will be essential.

In rainbow trout, our results were again different. We obtained no evidence for activity of the mosaic zone of the myotome during sustained activity even at 4.5 BL/s (the maximum speed at which we could swim the smaller fish). Considering Hudson's (1973) electromyographic evidence from the same species, where he observed activity from the mosaic zone at speeds above 3.0BL/s, this seemed at first rather surprising.

However, the fish Hudson used came from a stock of notoriously poor swimming performance (see Webb 1971), and it is therefore quite possible that we never attained the critical speed at which the mosaic muscle became active in our fish. The main muscle mass in rainbow trout consists of a mosaic of small reddish fibres scattered amongst larger pale fibres (Johnston et al. (1975) have studied them histochemically), and it is thus unclear whether the low-level electrical activity which Hudson (1973) recorded from this region (similar to that which we found in carp white muscle) comes from the same fibres as those generating muscle action potentials during burst swimming. In other words, the two kinds of electrical responses from the rainbow trout mosaic muscle may result from the activity of two different kinds of muscle fibres.

Fish are so diverse, and their patterns of life so varied, that it is hardly surprising that there should be differences on their locomotor musculature. We perhaps ought rather to be surprised at

the general uniformity of design of the locomotor system imposed by the aquatic medium. It seems probable, from the distribution of patterns of innervation amongst different fish groups, and indeed amongst the teleosts alone, that focally innervated, twitch fibres operating by anaerobic glycolysis for short bursts of swimming represent the primitive arrangement of the aquatic fast motor system (see Bone 1970).

This fast-motor system contrasts markedly with the universally found multiply innervated nontwitch red fibre system for sustained movement that operates aerobically. However, histological and biochemical investigations of the white myotomal zones of some specialized teleosts such as tuna (Guppy et al. in press) or carp (Johnston et al. 1977) have shown a definite aerobic capacity in the white fibre system, and the original simple dichotomy between anaerobic white fibres and aerobic red fibres rather naively suggested from elasmobranch studies (Bone 1966) is plainly not a good description of the operation of the myotome in all teleosts.

On the whole, it seems reasonable to assume that in most teleosts where the white portion of the myotome is multiply innervated, there will be aerobic intermediate fibres for use during fast sustained cruising, and that at the maximum cruising speed at least some fibres in the white zone of the myotome will also be active aerobically. This seems to be the situation in rainbow trout, and it probably also obtains in most scombrids.

The situation in carp is less clear. The work of Smit et al. (1971) has shown that goldfish (close to carp) are able to sustain high speeds in a respirometer apparently using the white muscle system anaerobically. In line with this, Driedzic and Hochachka (1975) were unable to detect other energy sources than anaerobic glycolysis in carp white muscle, and Johnston et al. (1977) only found low values of aerobic enzymes in this system. We have provided clear evidence that the white motor system is operating over a wide speed range, from the lowest speed at which the fish will swim in the respirometer, and it seems bizarre that a relatively inefficient anaerobic metabolism should drive sustained activity. At low sustained swimming speeds carp might keep in overall aerobic balance by transferring lactate from the white zone to other regions of the body, where lactate could be completely metabolized (Bone 1975). Driedzic and Hochachka found only low lactate levels in the white zone after severe

hypoxic stress, and suggested that this could be explained by lactate transfer out of the system. It is very hard to believe that such a process could account for the extremely interesting results of Smit and his colleagues (Driedzic and Hochachka entitled their paper "The unanswered question of high anaerobic capabilities of carp white muscle"), and we agree with Johnston et al. (1977) in their conclusion that carp would appear to be an ideal species for studying the relationship between muscle design and locomotor function.

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QUENTIN BONE

Plymouth Laboratory
Marine Biological Association of the United Kingdom
Citadel Hill
Plymouth PL1 2PB, England

JOE KICENIUK
DAVID R. JONES

Department of Zoology
University of British Columbia
Vancouver, B.C., Canada V6T 1W5