

The Control of Movement in Water - Lessons from the Study of Fish Locomotion.

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Introduction.

A few years ago, the Oxford zoologist, A.C. Hardy, proposed that early man had lived a semi-aquatic life at some time. His main evidence for this idea came from the distribution of hair on the human body which could best be explained, in Hardy's opinion, as an adaptation to aquatic life.

We have little information about the life style of early man so Hardy's suggestion remains only an amusing idea.

We do know however that much further back in evolutionary time our ancestors lived their lives totally in water. Close relatives of those ancestors - the fishes - are available for us to study today and we can turn to them to see what special features are associated with aquatic living.

Fish as model systems for the study of locomotion control.

The way fish swim, and how their movements are controlled by the nervous system, is an interesting biological problem. But a study of these processes can provide us with more than information just about fish. Because of the evolutionary link between our ancestors and modern fishes a study of the coordination of movement in fishes can reveal to us some of the principles of operation that are common to all vertebrate animals.

Further, fishes enable us to study the vertebrate locomotory system simplified in three ways, as compared with mammals. First, although the nervous system of a fish is built to the same plan as that of other vertebrates, it contains far fewer nerve cells. Second, there are fewer separate muscles in the body of a fish and so their control is simplified. When you consider, for example, the human arm and hand you will appreciate that it contains more separate muscles than are found in the whole body of a fish. Moreover, when moving our limbs, antagonist muscles must first retard the ongoing movement before driving the limb in the opposite direction. This damping function in fishes is provided externally by the water in which they live. Once again, the consequence of this will be to simplify motor control. Finally, in fishes, we see a locomotory system that is freed from the problems of posture. Postural control is immensely important for a land-living animal and many neurological problems involving human movement reflect the requirement to keep the body upright and to resist the pull of gravity. This is much less of a problem for fishes because they live in a dense supporting medium. These simplifications make the fish locomotory system an interesting "model" for us to study and from which to draw principles of operation. To do so effectively, however, it is important to appreciate these features that are similar to and those that are different from other vertebrates. The locomotory machinery

of fishes consists of the musculature, and the sensory and motor nerve supplies and we shall now describe these briefly.

Locomotor muscles and their nerve supply.

The body musculature of fishes is made of blocks, the myotomes, separated by connective tissue. Within these blocks, individual muscle fibres differ in size and function. There are two main types which can readily be seen in any freshly caught fish because they differ in colour. The outer border of the myotome, just beneath the skin, contains red muscle fibres, full of myoglobin, which are used for cruising swimming. They surround a much larger mass of white muscle fibres which are for higher swimming speeds. Each red fibre contracts slowly, does not fatigue and is innervated by several nerve fibres, so it can contract in a graded fashion. In contrast, white fibres contract rapidly throughout their length and easily fatigue. In "primitive" fishes, such as the dogfish, they are supplied by only a single nerve fibre, an arrangement found in the muscles of nearly all vertebrates, but for some reason in more "advanced" fishes, such as the goldfish, many nerve fibres innervate individual muscle fibres.

The locomotory sensory system of fishes.

A fish swimming through water obtains information about the external world from a whole range of sense organs smell, sight, hearing and so forth. These sense organs do not immediately initiate locomotory movements. But other sense organs provide information that has an immediate impact on movement. These are the organs of balance and equilibrium of the ear, that work in conjunction with visual information, and the sense organs of the body - the proprioceptors. The ear of fishes is essentially similar in design to that of all other vertebrates for only the cochlea, the hearing organ of reptiles, birds and mammals is absent.

Semicircular canals respond to head accelerations and the receptors inform the fish of its position in space as it swims through the water and initiate correcting reflexes that maintain a steady course. For example when a dogfish rolls about its longitudinal axis, the pectoral fins are moved to compensate for the deviation. Thus, if the roll is to the left, the right fin moves down to oppose the roll. These important compensating reflexes are essential for the equilibrium of the swimming fish and depend on sensory detectors in the ears. The inner ear of fishes is very similar to that of mammals, but the other locomotor sense organs, the proprioceptors, are much simpler. In contrast to terrestrial vertebrates where there is a considerable range of morphologically complex proprioceptors situated amongst the muscle fibres, in tendons and joints, to register muscle length and tension and angle of the limbs, the fishes have only a very limited number of locomotory sensors. In particular, the muscle spindle which is important in mammals for certain reflex movements has only been reported in the specialised jaw muscles of fishes and appears to be absent from the body muscles. These spindles,

which are found in the muscles of amphibia and other vertebrates, are probably a feature of terrestrial life and the accompanying increased loading on the body. Two types of sensory endings have been described in sharks and rays. One, an intramuscular ending of the pectoral fins of skates and rays, has physiological properties that are similar to the responses of the muscle spindles of frogs and reptiles. The other receptor has been found in the body of sharks and lies beneath the skin, outside the musculature, and measures the bending movements of the body.

The nervous system of fishes.

At first sight the brains of fishes and mammals appear to be very different in shape and size. A human brain weighs some 1.4 kg and contains perhaps one hundred thousand million (10¹¹) nerve cells. The brain of a fish is very much smaller and contains far fewer nerve cells, yet the way these are organized within the brain is essentially similar to the arrangement found in mammals. The main differences are seen at the front of the brain, where the very large, folded cerebral hemispheres dominate the mammalian brain. This part of the brain seems to be responsible for thought processes, memory and emotion. Damage to this region in man certainly disturbs locomotion but the basic processes of movement are regulated by other regions of the brain, and many of these are found in the brains of fishes. Thus the spinal cord, the brain stem and cerebellum can all be easily recognized in the fish brain. And it is in the spinal cord, that in all vertebrates the basic locomotory programs are established.

The spinal cord and locomotion.

The movements of a swimming fish result from waves of contraction of the body muscles that pass down the body and throw it into propulsive waves that accelerate the water adjacent to the fish's surface. How is this pattern of muscular activity produced? We know that the basic features of the locomotory movements are produced within the spinal cord. We can say this with some confidence because a dogfish with a severed spinal cord continues to swim. Indeed, if we remove the brain of a dogfish completely so that only the spinal cord remains, and keep the blood oxygenated, the resulting "preparation" will "swim" for hours. The movements are slower and less powerful than normal and do not propel the fish, which in any case has no abilities to maintain its balance. This "spinal locomotion", of course, is in complete contrast to what we see in paraplegic humans who perform no locomotory movements. The dogfish is unusual in that it displays this spinal locomotion immediately the cord is cut. In other fishes, such as the eels, spinal swimming occurs some time after the cord has been severed.

Electromyographic recordings from wires placed in the red and white musculature show that only the red fibres are active during this steady swimming. But the white fibres become active if, for example, the tail is pinched. The recordings

also show that the muscles are activated in a sequence, the more rostral myotomes being active before the more caudal, while myotomes on opposite sides of the body are never simultaneously active. This pattern produces the passage of muscular contraction along the body. If we now expose a bundle of motor nerves that supply the muscle fibres and draw it into an electrode, we can study the output of the spinal cord during locomotion.

As we would expect, we find that the motor nerves are discharging regularly, to drive the swimming muscles.

Motor nerve cells on opposite sides are active alternatively and in a timed sequence along the body.

Where does the motor pattern come from? Clearly, it does not come from the brain, for that has been removed! It arises within the spinal cord and could involve either spontaneously active "pacemaker" nerve cells, or require input from proprioceptors stimulated by body movement. We can eliminate this feedback by stopping all movement of the body by injecting the muscle paralyzing drug curare. After curare injecting we see in our recordings that the motor nerve cells continue to send rhythmical bursts of signals to the inactive muscles. The pattern of the activity is the same as before, but the rhythm is slower. So we see that the spinal cord in the spinal dogfish preparation can produce the appropriate motor patterns internally, without reference to external activities. Indeed in another fish-like vertebrate, the lamprey, patterned motor activity can even be recorded from isolated pieces of the spinal cord, maintained in physiological solutions in an experimental bath. However, it would be wrong to conclude that this result means that sensory feedback is unimportant for locomotion, because it in fact plays a very significant role. The impact of sensory feedback during locomotion can be seen in experiments on the paralyzed spinal dogfish preparation for if we bend the body of the fish in a way that imitates body shape during swimming, we can see in our nerve recordings that the motor output from the spinal cord immediately changes its rhythm and follows that of the feedback. This following action we call "entrainment" and it is a very important process within the central nervous system. It reflects the interaction of one oscillating system with another. The meaning of this feedback for the "real" fish, swimming in the sea, would be to stabilize the activity of spinal cord circuits and to prevent them become erratic, or disrupted by other irrelevant sensory signals.

The role of the brain.

The spinal dogfish lacks the potential for organized changes in locomotor performance which characterise the intact fish. In response to cutaneous stimulation, body movements become faster, or if the white muscles are activated, much stronger, but that is all. An intact fish shows a much wider range of locomotory behaviour and strategies and produces fast turns, speed changes and gliding. These more complex movements require action within the brain.

Consider a trout swimming upriver. It has to change speed as

the river flows faster or slower. We can see how this is done if we put a trout in a tunnel of flowing water. The trout beats its tail to maintain a steady position in the tunnel and as we change the water speed, the trout still remains "on station" by changing the tail-beat frequency. To do this, the trout detects the changing water flow and modifies the performance of the locomotor generators in the spinal cord changing the frequency of the motor rhythm so as to maintain its stable position. Information from the eyes indicates if the external world is stationary or moving; if moving then an "optomotor" response is generated, to compensate for the movement. The fish also "feels" the water flow over the head and body using tactile receptors. This information is also channelled into the brain to modify the spinal cord systems.

In fishes, the nerve cells that connect the brain to the spinal cord lie in the brainstem for unlike mammals there are no direct connections from the forebrain to the cord (i.e., there is no "pyramidal" system). Some of the brainstem nerve cells connect directly with the motoneurons of the spinal cord and, when active, they bring about rapid body movement, of the kind required for turns and acceleration, such as are seen in "escape" movements. Other brainstem neurons, however, connect indirectly with the motoneurons, going on to the interneurons responsible for the motor rhythm.

The brainstem nerve cells are connected to other brain centres which control the spinal networks. One of these centres is the mesencephalic locomotor region.

The mesencephalic locomotor region.

If the forebrain of a cat is removed, the resulting decerebrate preparation is unable to move spontaneously. But if stimulating electrodes are located in a specific part of the mid-brain of a decerebrated cat - the mesencephalic locomotor region - locomotory-type movements can be initiated and regulated. Continual electrical stimulation of a limited region of the midbrain of the goldfish will also evoke coordinated swimming movements of the caudal and other fins.

Movements can be modified by changing the strength of stimulation: weak stimulation triggers movement of the pectoral fins while stronger stimulation brings about movements of the tail as well. The frequency of the fin movements is also dependent on the strength of stimulation. These results suggest that there are regions of the brain which are directly controlling the spinal circuits, selecting and combining the "program" for locomotion.

The cerebellum.

The activity of brain stem neurons is regulated by the cerebellum. The cerebellum is a large brain structure in fishes which has exactly the same construction as the mammalian cerebellum, with the same cell types organized in the same arrangement. The photograph of the longitudinal section through the brain of the porbe aple shark emphasises the resemblance to the mammalian cerebellum.

The earliest attempts to understand the cerebellum relied on ablation, and in fishes this approach gave very confusing results. This was not only because of differences between techniques but also because some workers have expected the profound locomotory disturbances of the decerebellated mammal to be seen in fishes. In fact, closer examination of the mammalian results suggest that the underlying cause of the locomotory disturbances is the disruption of postural control which as we have seen is simplified in fishes. Long ago Luciani observed that a decerebellate dog, though unable to stand, could swim normally when placed in water and other workers have also found that mammalian swimming movements are little disturbed by cerebellectomy. Therefore, in this context, the reports of limited effects of cerebellectomy in fishes are not surprising.

Present evidence suggests that the function of the cerebellum is to regulate the descending excitatory and inhibitory pathways going to the spinal cord. Consequently, if the cerebellum is removed, the movements of the fish are greatly reduced in amplitude so that in a water tunnel a swimming decerebellated trout cannot sustain movement at the higher water speeds. The fish behaves as if there is some kind of brake applied to the locomotory system.

The higher centres.

We have very little information about the role of other brain centres in the control of locomotion in fishes. If the fore-brain is removed from a fish, the basic locomotory behaviour is unchanged - in fact it is difficult to observe any obvious difference in behaviour. It seems that these brain regions are for the analysis of sensory information about the world, for comparison with stored memories and for the development of complex programs for hunting, sexual behaviour and so forth.

Locomotory control in fishes and comparisons with other vertebrates.

We can now review our story so far, so as to establish a general pattern for locomotory control in fishes and to compare this with what is known in other vertebrates, especially mammals.

The basic program for locomotion is produced within the spinal cord. It depends on the spontaneous activity of certain nerve cells and on sensory information derived from receptors in the skin. This basic program ensures that antagonistic muscles work in opposition and at the correct times. Swimming speed is changed by commands descending from the brain which increase or decrease the activity of the spinal cord circuits. These commands are selected by higher centres in the brain and are combined to give behaviourally relevant locomotion.

In comparison with the organization seen in fishes, movement control in mammals seems much more complicated. Certainly, with the development of limbs, there are many more muscles to control and therefore more separate sets of commands are required within the motor program. With loading on the limbs,

sensory information comes not from the surface, but from deep within the muscles, or across the joints. Some muscles must be continually active - the phenomenon of tone - to provide posture and balance. But some features of locomotion are still derived from within the spinal cord, and the spinal mammal when suitably treated with certain drugs can carry out some regular hind limb movements. The spinal cord centres are driven from the brainstem controlled by the cerebellum. All this gives us the impression that the mammalian picture is a much more complex version of that seen in the fish, but certain basic themes can still be recognized.

This conclusion encourages us to continue to study brain mechanisms in fishes, in an attempt to determine the basic principles of control in vertebrate animals. Further, it makes us think about the possibility of finding a way of making the injured nervous system repair itself. For, when the spinal cord of a fish is severed, paralysis of movement results, but with time and in complete contrast to the situation in ourselves and other mammals, locomotory movements of the body recommence as the spinal cord repairs itself. This does not happen in humans, but perhaps it can.