 #346

FARADAY'S ELECTRIC EEL
Part Two: An Undulatory Life*

I
What really moves a self-mover?

Since Newton's first publication of his Laws of Motion in the *Principia*, generations of mathematicians and physicists have continually reformulated them with the aim of making the Laws more algebraic. In the process, they departed from Newton's own understanding in significant ways. But with respect to a certain articulation of *activity*, the modern conventional expressions not only preserve but even fortify Newton's rhetoric.

If we ask what it is that actually moves a body, Newton's First Law of Motion would seem to implicate an *impressed force*. Here is how one classic textbook states it:

> "Every body persists in its state of rest or uniform motion in a straight line unless it is compelled to change that state by a force impressed upon it."

Notice that this Law neither requires nor encourages us to specify the origin of the force. It is said simply to be "impressed upon" the body and is, otherwise, wholly anonymous. The force might arise from being struck with a rock, or from the disdainful sweep of some hero's hand. It could be one of those mysterious forces that act "at a distance," like magnetism and electricity, and perhaps gravity. It could be the finger of God. In all these cases the force is external to the body that is moved.

Now there is nothing wrong with this imagery of activity so long as we are talking about bodies that are inert and inanimate. But such rhetoric becomes troublesome and embarrassing when we attempt to apply it to a *self-mover*.

Consider the act of walking, for example. [SLIDE 2] As illustrated in this sketch,[1] the walker is striding forwards. Now even the steadiest of walking is not "uniform motion in a straight line"; so we can infer that some *force* is being impressed upon the walker, at least at such moments as the one pictured here. And unless we think he is being whisked along by some unknown and distant agency, that force must be acting by *contact*. Nothing, however, is in contact with the walker except the earth; and *that*—at this moment, at least—only at the ball of the right foot. The conclusion appears inescapable: It seems we are going to have to identify *the force applied to his right foot* as "that which moves the walker."

Slide 2

But this seems just silly. The walker is surely moving *himself*. Nobody wants to say that it is some external "force" that propels him. And if we try to avoid an

---

* This talk was presented in Santa Fe on April 26, 2006. Part One, "The Body Electric," was given in Annapolis in October 1991 and in Santa Fe on March 29, 2006.

anonymous externality by ascribing that force to the *earth*, it will only make matters worse. Surely it is not the earth that is moving the walker! The earth does not spontaneously nudge living creatures from place to place, like chess pieces, along its surface.

It is at this point that students of animal motion begin to find some comfort in Newton's Third Law, which speaks a little more explicitly about the external agent. Quoting now from another textbook, we state it this way:

> "If one body *acts* upon another by applying a force to it, the second body will *react* by applying an equal and opposite force to the first."

This Law tells us that application of force is always reciprocal, so that forces come in pairs. Either member of the pair may be called the *action*; and then the force that is reciprocally applied will be called the *reaction*. With the aid of the Third Law we can offer a more acceptable analysis of our earlier walking example by noting that, if the earth is applying a force to the walker's foot, the foot must likewise be applying an equal, oppositely-directed force to the earth. We may therefore call the force that the *foot* applies the "action"—thereby preserving the role of the walker (or at least the walker's organ of locomotion) as the agent. The force applied by the earth is then the "reaction"—a term that no longer appears to ascribe volitional or spontaneous motive power to the inanimate earth.

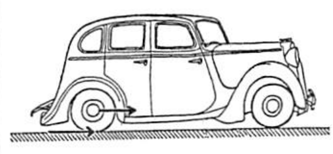
We might ask: If physicists have been so willing to reformulate Newton's laws of motion in the past, why haven't they done so in a way that would make this last interpretation more evident? Well, one of them has. Sir James Gray, in his wonderful book *Animal Locomotion*,[2] offers this charmingly zoöcentric statement of the First Law:

> "...if an animal is to move its body by its own unaided efforts, it must elicit a force from its external environment..."

Gray's rendition of the Law continues further, but let's consider only this fragment. In the phrase "elicit a force from its external environment" lies the desired interpretation of the animal as the agent of its own motion, and the consequent identification of the environment as merely reactive mechanically. Stated this way, it also reminds us that self-movers inevitably have to work *against* some medium.

With this in mind, let us examine the action of walking once more, [SLIDE 5] this time focusing on the organ of locomotion. The leg *is* an organ of locomotion because it is a site of conversion of chemical (that is to say, nutritional) energy into mechanical energy. When its muscles contract, such energy conversion is taking place. Our earlier walker "elicited a force from his environment" by pivoting and extending his leg; and so long as the leg maintains a reasonable firmness, that forward force will be transmitted through it to the hip joint, and ultimately to the rest of the body.

Slide 5

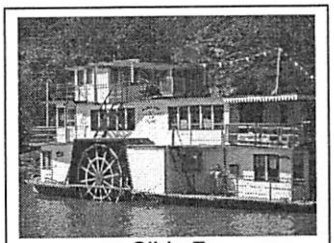

Slide 6

We could give a strikingly similar account of another self-mover, the appropriately-named *automobile*. [SLIDE 6] An automotive vehicle's engine and drive train are its organ of locomotion, being the site of conversion of chemical energy (in the fuel) to mechanical energy at the drive wheels. The automobile too "elicits a force from its environment" by rotating its powered wheels against the ground; and so long as each wheel maintains reasonable rigidity and does not slip, that force will be transmitted to the axle and suspension and ultimately to the whole vehicle chassis.

So we have considered two self-movers, only one of them animate, but both possessing organs of locomotion. Now which organ shall we say most constitutes a standard for the other? Shall we say that the powered *wheel* is merely a clever imitation of a set of legs? Or shall we hold that the animal *leg* is nature's attempt to emulate the circular motion of a wheel? What, in short, is the paradigm for animal locomotion?

If we are feeling particularly Greek in our thinking, we might suppose that animal locomotion ought to be viewed as derivative from circular motion—especially the celestial circular motions, and ultimately the first motion produced by the prime mover. Of course Aristotelian astronomical motions do not involve expenditure of energy, whereas animal locomotion does. Moreover celestial circular motion is continuous and homogeneous. It is not divided into distinct segments or phases; on the contrary, every segment of pure circular motion is identical with every other equal segment.

By contrast the act of walking, while certainly cyclical (in the sense that it involves *repeated* actions), also exhibits a clear distinction of *phases* that are not homogeneous. After an initial preparatory placement with respect to the ground and the rest of the body, the walking leg executes a power stroke that propels the body forward; but afterward the leg has to restore itself to the prepared condition before it can execute another power stroke. The power stroke of a leg or limb requires contact with the ground; but during the restorative phase the foot or paw is lifted from the ground and moves through the air. Needless to say, if the limb were not lifted, a leglike organ would only be able to rock an animal back and forth, it could not bring about progression. Animal locomotion, then, appears to be governed by two principles; first, *cyclical action*, a principle it shares with the heavens. Second, at least in a great many animals, *inhomogeneity of phase*, a principle sharply in contrast with the heavens.


Slide 7

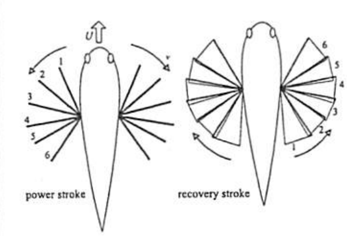
In general, things that move along the surface between two different media will exhibit both these principles. A boat is rowed, and a canoe is paddled, by means of an organ that operates cyclically, but whose cycle is divided into a power phase (in the water), followed by a restorative phase (in the air). [SLIDE 7] The paddle wheel of a riverboat is the same; each of its paddles alternates between a power phase while it is submerged in the water and a restorative phase as it returns through the air.

Even landgoing wheeled vehicles exhibit this same duality of phase. [SLIDE 8] Every point on a wheel, at least on a physical wheel, alternates between a phase of contact with the ground—the power phase—and a return phase through the air. For a typical automobile tire such as the one shown here, the power phase might represent about 7 inches (marked in the photo by chalk lines) out of a total circumference of 75 inches. So surface-moving vehicles are rather similar to surface-moving animals, in respect of the principles of their "organs" of locomotion.


Slide 8

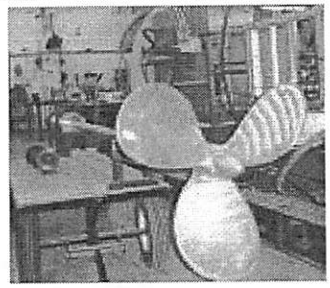
But what about creatures like birds, flying as they do in a single medium? The wing, like the leg, executes a cycle that consists of a power phase alternating with a restorative phase. However since both phases of a wing's action must occupy the same medium—the air—birds must distinguish those phases by some means other than by exchanging media. They do so by changing the configuration and orientation of their wings. During the power stroke the wing presents a high cross-section area and moves at a high velocity, consequently developing a high viscous force against the air. During the return phase the wing may present either a lower cross-section area, or a lower velocity, or both. It consequently experiences relatively little air resistance as it prepares for the next power stroke. Airborne vehicles, however, do not resemble birds in this respect. The revolutions of an airplane's or a dirigible's *propeller*, while indeed cyclic, are nevertheless *not* divided into power phase and restorative phase. A propeller fans the air without respite and thus provides a continuous thrust to the vehicle.

Fishes, too, are confined to a single medium. Unlike birds, in many fish species the whole body participates significantly in maintaining locomotion, besides employing specialized appendages such as fins. [SLIDE 9] Nevertheless the pectoral fins of many fishes resemble the wings of birds in their action, alternating between high velocity power strokes and lower velocity return phases, along with appropriate changes in fin configuration and orientation.[3] Fishes that swim this way are said to exhibit *labriform* motion. But here again, manmade vehicles differ. Propeller-driven submarines, for example, develop a continuous thrust; they do not exhibit the alternation between power phase and restorative phase that we find in a pectoral fin.



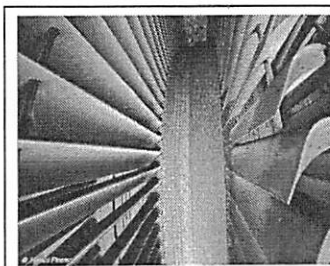
Slide 9

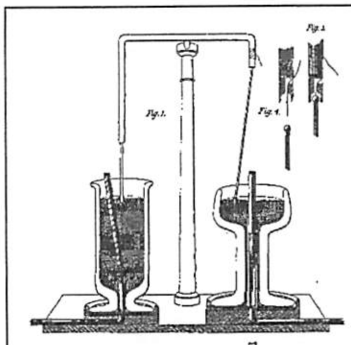
Propellers, or screws [SLIDE 10], would appear to emulate the celestial circular motions far more closely than do the appendages of animals. While, to be sure, propellers do exert *thrust*, which the astronomical prime mover does not, their circular motions are just as homogeneous as those of the celestial spheres; they are not divided into alternate phases of effort and restoration. So why don't fishes and birds have propellers?


Slide 10

Well, it is clear that in order to achieve continuous rotation, *sliding surfaces* are required between the rotating structure and the body as a whole. Moreover, *mechanical energy* has to be capable of crossing the boundary between the fixed and moving surfaces.

Energy flow across a moving boundary is no problem for manmade engines. [SLIDE 11] In the steam turbine, for example, expanding steam fills the space between the stationary housing and a *rotor*, shown here in a photograph. The rotor turns under the consequent pressure; mechanical energy has therefore passed from the stationary to the moving element. For another example, the rotary windings of one form of electric motor receive electricity through metallic "brushes," which make a continuously sliding contact with wires from the stationary battery. Faraday's electromagnetic rotator [SLIDE 12], which some of you may have seen in Junior Lab, was perhaps the first such "motor" to employ this principle. The version on the right in this picture is easiest to interpret; in it, electrical energy passes to the moving rod through a sliding contact at its suspension, above , and at the liquid mercury bath, below .


13: Slide 11


Slide 12

Another kind of electric engine, the induction motor, does not even require contact; in it, magnetic energy passes from the stationary field winding to become mechanical energy in the rotor. We see, therefore, that energy exchange between a stationary surface and a continuously revolving surface is not an obstacle for inorganic matter.

Living structures, however, cannot survive just by exchanging energy with their surroundings. They must also exchange *material.* Living tissue has to carry out metabolism; it must receive nourishment and expel waste. Animals above the microscopic level appear to require systems of *permanent attachment*—things like vessels and tubes—to do this. Metabolism is thus the enemy of circular motion. As we should not expect to find metabolism going on in the vicinity of the celestial spheres, no more should we expect to find continuous circular motion exhibited in terrestrial living creatures.

Nevertheless there exist animal species that come as close as any living body can to solving the problem of circular motion—to having wheels, as it were. They are, nearly all of them, fishes; and they progress by executing *traveling wave motion.* Let me review briefly why wave motion is so closely allied to circular motion.

To do so I will make use of a few toys. The first is just a disk, having an axle through its center and a peg mounted eccentrically. I have oriented the disk vertically on the transparency projector, so that when I cause it to rotate, we can see the shadow of the eccentric peg executing simple harmonic motion—the motion of a pendulum. Juniors and seniors will recognize this device—affectionately, I hope—as the Paradigm Circle. Sophomores will see it as

Ptolemy's epicycle, which carries an inner planet through its alternating eastern and western elongations.

Now I want to make a little change. Instead of passing an axle through the disk's center and making the peg eccentric, I will make the *axle* eccentric and place the *peg* at the center—which clearly ought to result in the same pendular motion as before. Or rather, instead of attending to the disk's center peg, we can observe the shadow of the disk's *circumference.* Since every part of the circumference is a constant distance from the center, whatever motion the center undergoes, the shadow of the circumference will show *exactly the same motion.* Here I set the eccentric disk into rotation; and sure enough, we see the shadow of the circumference oscillating back and forth, just as the eccentric peg had done previously. So the eccentric disk is a paradigm circle, too.

Now what happens if I arrange a series of eccentric disks side by side on the same axle? Obviously if they are all just lined up with one another, like this, they form in effect a cylinder having an eccentric axis. When that cylinder is rotated, its shadow exhibits pendular motion as a whole, as you see. But there is nothing particularly exciting about that; an eccentric cylinder is hardly different from an eccentric disk.

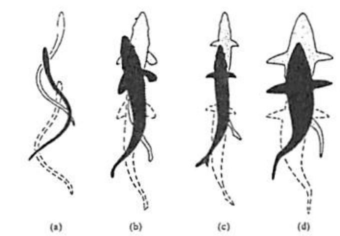
But here you see another array of eccentric disks skewered on a single axle—only I have turned each disk around the axle a few degrees more than its neighbor—a little like the camshaft of an automobile engine. I have in this way set up what mathematicians call a *constant phase difference* between successive disks. When the array is set in rotation, the shadow of each disk will exhibit simple harmonic motion on its own. But at any moment, each disk will be a few degrees further into its cycle than its neighbor. You can see therefore that whatever displacement one disk undergoes, the adjacent disk will have done the very same thing a moment later—and then the one after that, and the one after that, and so on. Thus a certain transverse displacement will travel successively along the line of disks. *This is what we mean by a traveling wave.* Here I am turning the array of disks and you can see the shadow forming a wave pattern that appears to travel parallel to the axle, perpendicular to the individual disks—or, as I would prefer to call them, the individual *paradigm circles.*

I'd like you to take note of something else too, which will prove to be important later on. I am turning the crank clockwise, and the waveform appears to be moving away from my hand. If I reverse the turning action, the waveform likewise reverses its direction of travel. Notice that the whole waveform starts, stops, or reverses at once. That is of course only to be expected since the individual paradigm circles are constrained to start, stop, or reverse simultaneously.

Thus if a fish, or any animal, executes wave motion, that creature will be exhibiting a most fundamental aspect of circular motion. Yet its body will not have to incorporate continuously sliding surfaces incompatible with metabolism. The animal's body structures need only be capable of waving back and forth. Flexibility, not sliding, is all that such a body requires. Let us look, therefore, at some of the ways fishes *do* sustain wave motion.

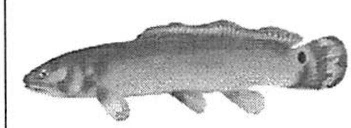
Section II
Fishes that Wave

Among other criteria, the locomotory modes of fish may be classified according to how much of their bodies participate in waving. [SLIDE 13] In what is called anguilliform motion, a fish's whole body undulates, as in drawing (a). In thunniform motion, on the other hand, oscillation is essentially confined to the tail, as shown in (d). Sketches (b) and (c) illustrate gradations between those two modes.[4] In this ranking we see the wave action being confined to a lesser and lesser fraction of the body's length.

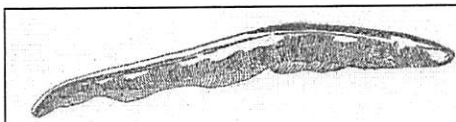


Slide 13

Other species manage to separate their wave activity from the body altogether, exporting it instead to specialized appendages. An example is the bowfin [SLIDE 14], whose elongated dorsal fin you can see here. This "ribbon fin" supports the fish's propulsive wave action, while the creature keeps its body proper relatively unbent.


Slide 14

Faraday's electric eel has no dorsal fin [SLIDE 15]. As I mentioned in my talk last month, it was for that reason called Gymnotus—"naked back"—in Faraday's time. The animal has since been reclassified, however; the accepted modern name is *Electrophorus electricus.* Electrophorus's anal fin is very long; and the creature propels itself by sending a traveling wave in the appropriate direction along the fin—towards the tail when it wishes to glide forward, toward the head when it wishes to back up. This species of movement is called gymnotiform locomotion, and it is found exclusively in *electric* fishes. This raises a question: Why would there be any connection between a creature's capability for electric generation, on the one hand, and its mode of locomotion, on the other?


Slide 15

We will return to that question later; but first I'd like to show you some video clips that reveal Electrophorus's wave action quite clearly. They are taken from a 2001 British documentary, and I believe they are the first electric eel movies ever to have been filmed not in an aquarium, but underwater in the Amazon River, which is the animal's native habitat.

[0:04] Practically the first thing we see here is the fish performing rapid reversals of the wave direction along his anal fin, just like the reversals I showed you with the "camshaft" device.

[0:12] See here what a huge wave amplitude he can develop!

[0:18] What I notice here is how loose and floppy the fin sometimes seems to be.

[0:30–33] Here are more wave reversals, and more instances of a "floppy" appearance in the fin.

[1:22–24] Here we just saw him *change* his wave velocity. It was speeding up and slowing down, but without reversing. We'll see more such instances in a moment.

[1:40–43] He is changing his wave velocity again here, though you have to look carefully to make it out.

[1:53] More wave reversals.

[2:37] Here you might be able to see the waveform taking on a somewhat "flattened" shape.

[2:50] These shots were taken in a laboratory tank, as you can see. There are a few other gymnotiform species present

[3:00] The little fish at the center appears to be Eigenmania. If you watch the mature Electrophorus in the foreground you can see him changing his wave velocity here too.

[3:18] This is a black ghost knifefish—the one that seems to be hanging vertically at the center of the screen.

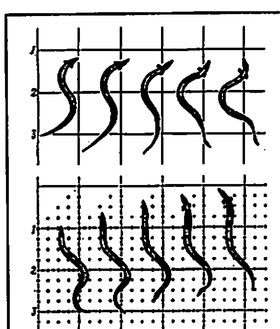
[3:37] The electrophorus has stunned a baby catfish and is trying to eat it. That won't be easy, since the catfish's spines prevent him from being drawn smoothly into Electrophorus's gullet.

[4:10] He is still trying to swallow the catfish. Since Electrophorus doesn't have any teeth, he either has to swallow the fish whole, or not at all. You can see how important his maneuvering ability is for this difficult job. Of course he would not have nearly so much trouble with his usual prey; the spiny catfish presents an exceptional challenge.

[4:46] Here again we see repeated reversals of his wave direction.

It is characteristic of gymnotiform locomotion that the propulsive effort is confined almost completely to the fin. Although Electrophorus's body is very flexible, we could see in the video shots that he tends to hold it in a nearly straight conformation while traveling in a straight path.

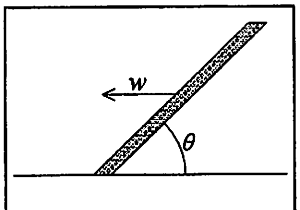
But how does the traveling wave "elicit a force from the environment" suitable for propelling the fish? It cannot be quite the same as what we described for land transport. When we walk, we seek good traction against the land surface; we don't want our feet to slip; but as we just saw, Electrophorus's propulsive wave generally *does* "slip"—that is, the waveform moves with respect to the water. The arches of Electrophorus's fin wave would like to brace themselves against the fluid medium, but they cannot. What would it be like if they could?


Slide 16

Sir James Gray actually approximated this situation with an eel [SLIDE 16]—I mean a true eel, whose entire body participates in *anguilliform* motion. When removed from water and placed on a smooth surface (upper half of this slide) ,[5] the animal produced undulations of very great amplitude, but he was unable to propel himself along the surface. Gray then studded the surface with smooth pegs; as you can see in the lower portion of the slide , the eel was able to brace the major arch of his wave shape against the adjacent pegs; by means of these footholds, as it were, he could propel himself forward among them.

But you cannot gain a steady foothold in water. The forces developed in fluids are viscous forces, which actually *require* relative motion between the fluid and the surface that bears the force. We experience this kind of force as the *drag* we encounter when we try to move an object through water. On the whole, the greater the speed through the water, the greater is the force developed; on the other hand, if there is *no* relative motion between the surface and the fluid, no force can be exerted. So you will see that in order to exert *any force at all* against the water, Electrophorus's wave surfaces will have to be moving with respect to the water—slipping, as it were. Thus he will not be able to develop the hefty forces necessary to accelerate or decelerate rapidly. On the other hand, his gymnotiform propulsion is just about the perfect means for slow trolling and hovering, because these actions call for forces that are modest and steady.

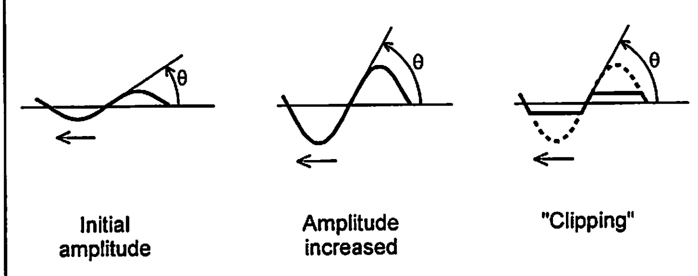
If you have ever paddled a canoe or kayak, you will have experienced another factor, besides its speed through the water, that determines how much force a moving surface will exert; that is its *angle of attack.* [SLIDE 17] A surface moving edgewise through quiet water experiences minimal drag; whereas a paddle that moves at an oblique angle will both exert and experience a greater force, for the same velocity. Now suppose we consider a small portion of Electrophorus's traveling waveform as if it were a flat surface making an angle θ with respect to his body, and moving at speed w through the water. This approach is really much too simplified to give numerical accuracy, but our purpose is only to identify some of the factors that control the force which the fin wave exerts. A straightforward calculation shows that the propulsive force is roughly proportional to the square of the wave speed w, divided by the cosine of the surface's angle θ; that is, proportional to $w^2/\cos\theta$.



Slide 17

So an animal like Electrophorus ought to be able to increase or decrease his propulsive force—and hence his body speed—by increasing or decreasing the speed with which he sends waves along his anal fin. And you will recall that we did see Electrophorus varying his wave speed considerably in some of the video scenes. Alternatively, he should be able to control his propulsive force by varying the angle of attack, a greater angle producing a greater force since its cosine in the denominator will be smaller.

Now in principle there are a number of ways to vary this angle. [SLIDE 19] One is to increase the wave amplitude relative to the wavelength, as shown in this slide. Comparing the first two sketches , you see that when amplitude is increased, the angle θ increases accordingly; and you will recall that one of our video scenes actually chronicled a fin wave having huge amplitude. But in other scenes we saw the fin take on a "flattened" contour,



Slide 19

as depicted in the third sketch . This resembles a waveform of large amplitude, but with the top cut off—what audio engineers would call "clipping" if it were a sound wave. By such means the fin achieves a higher angle of attack than it could have done using a sinusoidal waveform of the same amplitude.

Evidently, then, Electrophorus has a high degree of control over both the shape and the speed of his anal fin waves. This fact has far-reaching consequences. We are accustomed to thinking of waves as existing in or on an elastic medium under tension, as for instance a stretched string. In such media the velocity of wave propagation is determined, among other factors, by that very tension; for it is the elastic forces within the medium that couple adjacent elements together. If the forces between adjacent elements are strong (the case of high tension), their coupling will be close and the phase difference between adjacent elements will be small—that is, the motion of one element will follow quickly upon the motion of its neighbor, and the wave will propagate with high velocity. If on the other hand the elastic forces are weak (which is the case under low tension), there will be greater delay as each element passes on its motion to the next; the phase difference between adjoining elements will be larger, and the speed of wave propagation will be correspondingly smaller.

But look once again at a few of the video clips we saw before.

[4:57] Here again we see waves of extraordinarily large amplitude.

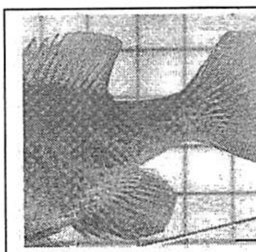
[5:03] Here the animal is rapidly reversing the wave direction; and notice that the *entire wave* changes its direction at once.

[5:15] We are continuing to see reversals of wave direction; but notice also the "floppy" appearance of the waveform.

[5:24] Here the fish that is further away from us is exhibiting the "clipped" waveform shape.

Does Electrophorus's anal fin appear to be a medium under tension? Far from it! It might give that impression when sustaining an energetic waveform; but when we notice the moments when it is *not* rapidly waving, the fin appears to flap loosely; it does not resemble a ribbon being stretched. How, then, does Electrophorus's fin support wave motion if it is *not* a medium under tension?

In fact the fin tissue is shaped not so much by forces of tension but rather by hundreds of bony ribs, or *fin-rays.* I'm sorry that I don't have a closeup view of Electrophorus's fin rays, but [SLIDE 20] here is a neat photo of those structures in a sunfish.[6] Electrophorus's anal fin, however, is far more flexible than the fins depicted here.


Slide 20

Each of Electrophorus's fin rays pivots in a delicate ball-and-socket joint[7] and enjoys its own share of the fish's ventral musculature. Now we saw in our review of wave motion and the paradigm circle that the individual elements of a traveling wave train must act successively. Each fin ray must on the one hand be under the control of its own paradigm circle, as it were; on the other hand those circles must be coordinated sequentially, just like the disks of the little mechanical toy I showed you earlier. But we saw that Electrophorus can *vary* his wave velocity, which means that he must be able to vary the phase difference between the fin rays' paradigm circles. In terms of our toy, this would mean that the individual disks cannot be rigidly coupled to a single shaft; for Electrophorus, it means that his fin rays must be mechanically independent of one another.

At the same time, we saw that when the fish reverses his wave motion, *the entire wave train stops and starts as a whole.* As our wave model showed, this means that the individual paradigm circles have to stop and reverse *simultaneously.* This would be easily achieved with a fixed mechanical coupling between successive fin rays, as it is in our toy. But since a fixed coupling between the rays has been ruled out, we must look elsewhere for the basis of a pattern of action that is *sequential,* on the one hand, but capable of *simultaneous* reversal, on the other. How can so adaptable a means of coordination be achieved?

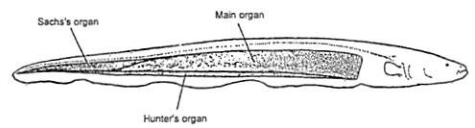
Two different modes of activity have been proposed. According to the first, the fin muscles are individually innervated, and they are stimulated in a rhythmic order that originates in, and is fully determined by, the central nervous system. The motor center of the nervous system keeps track, as it were, of each of the hundreds of fin muscles and issues to each its separate orders as to what to do and when to do it. According to the second proposal, a stimulus arriving at one end of the anal fin is actually transmitted from ray to ray along the fin, as peripheral sense organs in each muscle feel the activity of that muscle's immediate neighbor. Some forty years ago[8] the case between these views remained undecided—not only for the electric eel but for the undulatory motions of fish generally. Though it seems inconceivable that there would have been no more recent neurophysiological studies of this question, to my great surprise I have not been able to find any. We can see, however, that the second view—by supposing that the stimulus for action is passed successively from muscle group to muscle group—is incapable of explaining the *simultaneity* which, as we saw, is clearly demanded by the fish's wave-reversal activity. Moreover, according to that same view, the phase difference, and therefore the wave velocity, is controlled by an unknown neural coupling mechanism between neighboring fin-muscle groups. Unless the operation of that coupling is itself governed by the central nervous system, the animal's ability to vary its fin wave speed will remain unexplained.

If, on the other hand, the first view is correct, each fin-muscle group will have its own neural stimulus and therefore will be capable of cessation and reversal of motion simultaneously with every other muscle group. Moreover, the phase difference between stimulation of successive fin-muscles being under control of the central nervous system, it would then seem a straightforward matter for the animal to vary that difference, and hence vary the speed of the wave.

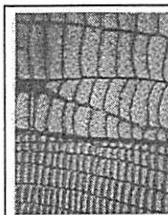
The first proposal—independent innervation of the fin muscles—would therefore appear to be the sounder one but—as I note again with continued astonishment—it does not seem to be a question that has excited fish anatomists to the extent that I would have expected.

Now in contrast to the meager attention being paid to the neurophysiology of Electrophorus's locomotion, there has been a veritable profusion of studies of his electric organs. Evidently those researchers who have been willing to take the trouble necessary to maintain one of these creatures have also been more interested in his electrical than his locomotory powers.

Let us, too, then, look more closely at Electrophorus's electric organs [SLIDE 21]—I use the plural, for he possesses three of them, as indicated in this sketch.[9] The organs designated "Main" and "Hunter's" generate the high-voltage shock impulses while Sachs's organ produces weak discharges. All three organs are composed of flat, muscle-like cells, termed *electrocytes,* [SLIDE 22] which are stacked in series like the metallic disks of Volta's electric pile. In this photomicrograph,[10] the cells of Sachs's organ lie at the top; the smaller, and vastly more numerous cells of the main electric organ are here at the bottom. The electrocytes are individually innervated; and when energized, each develops a small electrical potential of about 15 hundredths of a volt. This is only one-tenth the voltage of an ordinary flashlight cell; but in a large animal there can be as many as 4000 such cells in each "stack," which is enough to develop a very respectable total potential of some 600 volts.

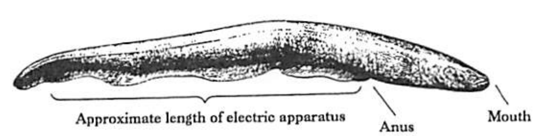


Slide 21


Slide 22

In the stacking of electrocytes we find an architectural theme of *serial repetition* that resembles the parallel ranks of bony rays that stiffen the anal fin. And just as the fin rays have to act simultaneously in order to reverse their traveling wave motion, the individual electrocytes have to act simultaneously in order to sum their potentials. This presents a problem in an animal whose electric organ is so highly elongated, for a signal traveling from the brain along the spinal cord will reach the anterior end of the organ significantly sooner than it can attain the posterior end. Special nerve architecture is therefore employed to achieve synchronicity. The neurons connected to nearer electrocytes take a long and circuitous path; and they are narrower than other neurons, which further retards the nerve impulses' arrival.[11] Individual innervation, then, seems to be the rule both for the electrocytes and for the muscle groups of the fin rays.

Electrophorus's locomotory and electric organs thus exhibit a common architecture of serial repetition, as well as occupying essentially the same portion of his body. [SLIDE 23] We have seen already that his propulsive anal fin is highly extended, running along about 80% of his total length. This is significant. By definition, a fish's anal fin arises at the anus and extends rearward towards the tail; so you can infer that the eel's anus—the terminus of his digestive tract—opens here, at about 20% of the body length. We might be tempted to say that it is this 20% that actually constitutes the *animal,* and that except for the fin, the rest is just batteries! Of course to say that would be to identify the animal proper with its *nutritive* life exclusively. Something like that was probably in Faraday's mind when he declared (I mentioned this in last month's talk) that the fish's electrical activity was—quote— "not the direct principle of *life.*"

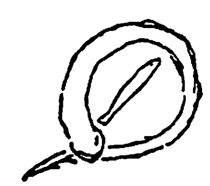


Slide 23

But perhaps Faraday's assessment is too narrow. For Aristotle, possession of locomotive ability stamps any organism as having more than a merely nutritive soul. On that view, Electrophorus's anal fin would be an essential element of his living nature. Might his possession of electrical apparatus similarly indicate *soul* in a richer degree? And would the affinity between his locomotory and electric organs imply some deeper functional relation between the two?

Let us consider the strong electric organs first. They serve both a predatory and a defensive function. The former office, at least, implies locomotion: predators *must* be able to move! Moreover since Electrophorus has no teeth with which to seize a struggling quarry, it is essential that he possess a capacity to paralyze or kill a potential prey. However, I don't see how we can argue that a predator—even an electrical one—needs to have a specific *kind* of locomotion; so the bare fact of predation does not, itself, indicate any special affinity between Electrophorus's electrical and his propulsive abilities. If such a connection does in fact exist, we would expect it to be manifest in some *specific* feature of the fish's activity. I believe we find this very thing in Faraday's "coiling incident," the circumstances of which I described in last month's talk.

Faraday, you will recall, had placed a live minnow in Electrophorus's tub [SLIDE 24]. Prior to shocking it, however, Electrophorus first encircled the fish with his own body; here is Faraday's sketch depicting that moment. As Faraday instantly recognized, the circumscribing action served to concentrate electrical power upon the unfortunate prey.



Slide 24

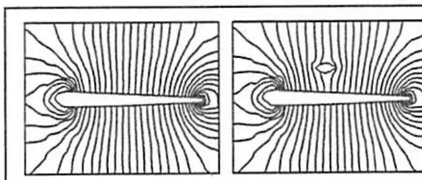
Now consider what is required of the electric animal in order to execute such a maneuver. He must *hold his body* in a curved position in order to concentrate the lethal power; at the same time he must *maintain his locomotion.* Electrophorus can do that because the propulsive movements of his anal fin are independent of the conformation of his body. In contrast, a trout, say—or any fish that propels itself by oscillations of the whole body—would have to cease locomotion if it kept its body in a fixed shape. Here, then, we see a very close functional connection between the animal's use of his strong electric organs, on the one hand, and his gymnotiform mode of locomotion, on the other.

An even fuller picture emerges when we look at the animal's weak electric organ. It produces electrical discharges that are readily detectible with proper instrumentation, but far too weak to stun or kill. All strongly-electric fish generate these feebler signals in addition to their lethal discharges; and there are very many weakly-electric species whose electrical activity is exclusively of this more delicate sort. Until about 1950 it was supposed that such weak electrical activity served no purpose, and animals whose electric ability did not rise to the level of combat were classified by some investigators as merely "pseudo-electric."[12] One wonders what they intended by the designation "pseudo." Such a dismissive epithet would seem to suggest a curious preoccupation with violence. Did this reflect some kind of Cold War mindset? Did they think that the only real electricity was *lethal* electricity? Well, we know now that, far from serving no purpose, the weak electric discharges are critical to their possessors' navigation, communication, and general sensory awareness.

In Electrophorus, and in many other species, the process works this way. First, with each weak electric impulse the animal establishes what we might call a "standard" field pattern in the water surrounding him. [SLIDE 25] You will remember how Faraday had showed that each of Electrophorus's strong electric discharges formed a sphondyloid-shaped field about the animal. Here is the informal sketch he provided in his Diary; I'll show you a more precise diagram in a moment. Not surprisingly, but gratifying nevertheless, Electrophorus's weak electric field exhibits a similar sphondyloid shape. At the same time, a series of "electroreceptor" sites distributed about the animal's skin sample the electric potentials at their own locations.

Slide 25

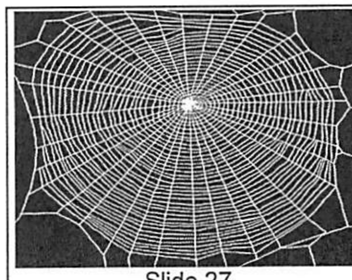
Now suppose some external object enters the field. If its electrical properties differ from those of water it will change the electrical potentials that develop in its immediate vicinity. [SLIDE 26] Here are two computer-generated diagrams that show the equipotential lines at the moment of electrification of a fish-shaped object. On the left we have the field in a completely uniform volume of water; on the right is the same field after introduction of an oval-shaped body more highly conductive than water; you see that the equipotential lines have been spread apart in the vicinity of the intruder. Had the body been instead a poorer conductor than water the equipotential lines would have been drawn more closely together.



Slide 26

Looking at these diagrams, you might well doubt whether Electrophorus could really detect the introduction of such an object. For while it is clear that the equipotential lines change their paths in the immediate neighborhood of the intruder, the lines' paths do not appear to alter *at the surface of the fish,* which is after all where the receptors are! But a principle that Faraday understood, and which Maxwell voiced more fully, corrects that hasty visual interpretation: If field conditions change *anywhere,* that change will be reflected *everywhere.* If it were not so, the field properties could not be continuous. So if the equipotential lines alter their paths adjacent to an intruding object, they must alter their paths at the animal's surface as well. The alteration may be minute, but it is real. It becomes then simply a question of the sensitivity of the animal's receptors, whether he can detect such minute changes or not.

The situation is not so different from that of the spider's web [SLIDE 27], which is an elaborate network of delicate fibers instead of a network of mathematical field lines. The web's overall shape expresses the mutual equilibrium of the weights and tensions of the filaments that compose it. We could think of it as a *field of mechanical tension,* comparable in its internal continuity to an electric field. Should some hapless insect alight at any point on the web, its weight alone, independently of its



Slide 27

struggles, would alter the distribution of tension not only in the adjacent strands, but in all of them. Real spiders tend to monitor these changes from the centers of their webs—a place particularly suited to the purpose. But *every* location on the web will reflect a new distribution of tension; and a sufficiently attentive Charlotte would know that something promising was afoot, no matter where on the web she happened to take her stand.

Electrophorus's electroreceptors are located along the whole length of his body surface. Changes in the distribution of potentials anywhere in the field will cause corresponding changes at each receptive location on the body—changes that will be slightly different at each site. The ensemble of conditions over the receptive area of the body may therefore be said to form a sort of "image" of the conditions in the surrounding field. Unlike optical images on a retina, this epidermal image is not *focused*—that is to say, the points which compose it do not exhibit one-to-one correspondence with points on an "object." Nevertheless we can readily see how this system can alert the animal to the presence of objects, perhaps even to an estimate of their relative size and location.

The system I have described is a *differential* one. As our earlier field diagrams suggested, the animal must constantly monitor differences between present conditions at his skin, and the conditions characteristic of the "standard" field that his electric discharges would produce in a uniform environment. Essentially, Electrophorus must monitor and interpret distortions of, and departures from, Faraday's sphondyloid.

You can see that this puts important constraints on the animal's behavior. If distortions in the sphondyloid pattern are to reflect external presences, it is important that the animal not introduce such distortions himself. For example, he ought not to bend his body, at least not while he is trolling for prey. As Faraday showed us, bending a bar-magnet will deform its sphondyloid pattern significantly; and the same thing will happen to the electric eel's sphondyloid should he bend his own body. Nor, while prospecting, should he suddenly speed up or slow down. Abrupt changes in his speed would complicate the patterns of differential change experienced at the electroreceptor sites, making interpretation less reliable. How suitable, therefore, is Electrophorus's actual gymnotiform mode of locomotion! By confining propulsive action to an anal fin, gymnotiform locomotion permits the overall body shape to remain straight and stable. As we also saw, the anal fin's traveling wave is ideal for establishing a slow, steady cruising motion but is comparatively ineffectual as a means of rapid acceleration.

We have gained, I think, a somewhat more accurate understanding of Electrophorus's body plan. His anterior 20% is, so to speak, the domain of his nutritive soul. His posterior 80% sustains higher, not lower, soul-aspects; it is where the animal projects himself into the world and is also, strikingly, the seat of his awareness of that world. We see too that the locomotory and electrical organs, together with their modes of activity, are admirably harmonized with one another. If we ever thought that Electrophorus's posterior body was just a kind of utility room where he keeps his batteries and hiking boots we cannot hold that view any longer. Nor, on the other hand, will we harbor fears that his electricity represents alien, unnatural, or demonic powers—a notion I mentioned in my previous talk and one that Faraday just about demolished. Electrophorus is instead a wholly integrated animal, and that wholeness fully encompasses his electrical capabilities. Such had been Faraday's vision—a vision, as is so often the case with him, that has proved to be both a fruitful and an elevating one.

Section III
"The Eel of Science"

That odd phrase seems to have originated with Erasmus,[13] but it is far better known from a passage in Pope's *Dunciad,* which I cannot resist reciting for you:[14]

> So spirits ending their terrestrial race,
> Ascend, and recognize their native place.
>
> ***
>
> Here to her chosen all her works she shows;
> Prose swelled to verse, verse loitering into prose:
> How random thoughts now meaning chance to find,
> Now leave all memory of sense behind:
> How prologues into prefaces decay,
> And these to notes are frittered quite away:
> How index-learning turns no student pale,
> Yet holds the eel of science by the tail.

That phrase, *the eel of science,* is a metaphorical genitive.[15] Science is an *eel* because it tends to slip from one's grasp the way an eel would wriggle out of the hand—especially if you *hold it by the tail,* that is, if you have a careless or uninformed grasp of the subject.

But we are in a position to see that Faraday's electric eel is an "eel of science" in the sense of the subjective genitive. Faraday's eel is "of science" inasmuch as it has proved to be a fitting and fruitful being for science to study. It has perhaps struck you that Faraday's electric eel is just about the perfect animal to associate with our Junior Laboratory. We are certainly in need of such an animal, since the Junior year is presently the *only* year that fails to include a major study of living beings in its laboratory curriculum. Faraday's electric eel is a living emblem of the work of that year. He represents both semesters: the *paradigm circle* and *wave motion* from the fall, and the *electric field* from the spring. And not only his body plan but his whole mode of life cooperate to present those topics in the full richness of their unity and coherence. Would that we might do as well, in continuing to craft the St. John's laboratory program!

H. Fisher

---

[1] Illustration after Edward Bawden in Gray, Sir James, *How Animals Move,* Pelican Books (1959)

[2] Gray, Sir James. *Animal Locomotion,* W. W. Norton and Co. (1968)

[3] Illustration from Sfakiotakis, M. et. al., "Review of Fish Swimming Modes for Aquatic Locomotion," *IEEE Journal of Oceanic Engineering,* 24, 2 (April 1999)

[4] Illustration from Sfakiotakis et. al., cit.

[5] Illustration after Edward Bawden in Gray, *How Animals Move* (cit.)

[6] Illustration from Standen, M. and G. V. Lauder, "Dorsal and anal fin function in bluegill sunfish *Lepomis macrochirus*: three-dimensional kinematics during propulsion and maneuvering," *J. Exper. Biol.* 208, 2753–2763 (2005)

[7] Albert, James S. and William G. R. Crampton, "Diversity and Phylogeny of Neotropical Electric Fishes (Gymnotiformes)," in T. E. Bullock, et. al., Eds., *Electroreception* (Springer Handbook of Auditory Research, 2005)

[8] Gray, *Animal Locomotion* (cit.)

[9] Drawing by John Langley Howard.

[10] Photomicrograph from Grundfest, H., "Electric Fishes," *Scientific American* (October 1960)

[11] Grundfest, H. (cit.). Since the problem of simultaneity exists for the fin-rays as for the electrocytes, one would expect anatomists to have ascertained whether similar neural architecture is employed in both cases.

[12] Grundfest, H. (cit.)

[13] Erasmus, *Adagia,* p. 324 (1629)

[14] Pope, Alexander, *The Dunciad,* Book I, line 279. Also in Smollet's *Peregrine Pickle,* chap. XLIII: "A mere index hunter, who held the eel of science by the tail." Closer to our day, "To hold the eel of science by the tail" was once, it seems, the motto of the Biology Department of Roanoke College.

[15] "Metaphorical genitive" is a term in Persian grammar ("*izafa-yi isti`ari*"). English grammar apparently does not recognize it (the nearest equivalent is the appositive genitive); but no other term seems to fit the present phrase's usage so well.