

Life at Low Reynolds Number

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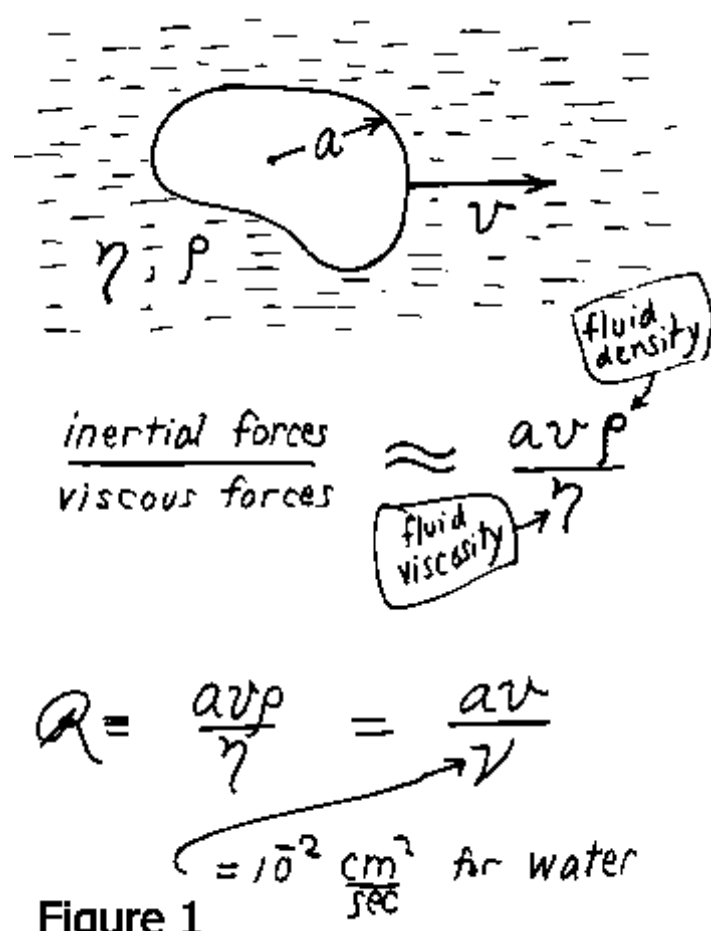
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Editor's note: This is a reprint of a (slightly edited) paper of the same title that appeared in the book Physics and Our World: A Symposium in Honor of Victor F. Weiskopf, published by the American Journal of Physics (1976). The personal tone of the original talk has been preserved in the paper, which was itself a slightly edited transcript of a tape. The figures reproduce transparencies used in the talk. The demonstration involved a tall rectangular transparent vessel of corn syrup, projected by an overhead projector turned on its side. Some essential hand waving could not be reproduced.

This is a talk that I would not, I'm afraid, have the nerve to give under any other circumstances. It's a story I've been saving up to tell Viki. Like so many of you here, I've enjoyed from time to time the wonderful experience of exploring with Viki some part of physics, or anything to which we can apply physics. We wander around strictly as amateurs equipped only with some elementary physics even if we don't throw much light on the other subjects. Now this is that kind of a subject, but I have still another reason for wanting to, as it were, needle Viki with it, because I'm going to talk for a while about viscosity. Viscosity in a liquid will be the dominant theme here and you know Viki's program of explaining everything including the height of mountains, with the elementary constants. The viscosity of a liquid is a very tough nut to crack, as he well knows, because when the stuff is cooled by merely 40 degrees, its viscosity can change by a factor of a million. I was really amazed by fluid viscosity in the early days of NMR, when it turned out that glycerin was just what we needed to explore the behavior of spin relaxation. And yet if you were a little bug inside the glycerin looking around, you wouldn't see much change in your glycerin as it cooled. Viki will say that he can at least predict the *logarithm* of the viscosity. And that, of course, is correct because the reason viscosity changes is that it's got one of these activation energy things and what he can predict is the order of magnitude of the exponent. But it's more mysterious than that, Viki, because if you look at the Chemical Rubber Handbook table you will find that there is almost no liquid with viscosity much lower than that of water. The viscosities have a big range *but they stop at the same place*. I don't understand that. That's what I'm leaving for him.



Now, I'm going to talk about a world which, as physicists, we almost never think about. The physicist hears about viscosity in high school when he's repeating Millikan's oil drop experiment and he never hears about it again, at least not in what I teach. And Reynolds's number, of course, is something for the engineers. And the *low* Reynolds's number regime most engineers aren't even interested in--except possibly chemical engineers, in connection with fluidized beds, a fascinating topic I heard about from a chemical engineering friend at MIT. But I want to take you into the world of very low Reynolds number--a world which is inhabited by the overwhelming majority of the organisms in this room. This world is quite different from the one that we have developed our intuitions in.

I might say what got me into this. To introduce something that will come later, I'm going to talk partly about how microorganisms swim. That will not, however, turn out to be the only important question about them. I got into this through the work of a former colleague of mine at Harvard, Howard Berg. Berg got his Ph.D. with Norman Ramsey, working on a hydrogen maser, and then he went back into biology, which had been his early love, and into cellular physiology. He is now at the University of Colorado at Boulder, and has recently participated in what seems to me one of the most astonishing discoveries about the questions we're going to talk about. So it was partly Howard's work, tracking *E. coli* and finding out this strange thing about them, that got me thinking about this elementary physics stuff.

Well here we go. In Fig. 1., you see an object which is moving through a fluid with velocity v . It has dimension a . In Stoke's law,

the object is a sphere, but here it's anything; η and ρ are the viscosity and density of the fluid. The ratio of the inertial forces to the viscous forces, as Osborne Reynolds pointed out slightly less than a hundred years ago, is given by $av\rho/\eta$ or av/ν ,

$$\frac{\eta^2}{\rho} = \text{force}$$

for water, $\frac{\eta^2}{\rho} = 10^{-4}$ dynes

This force will tow anything, large or small, at $R \approx 1$

Earth's mantle has $\eta \approx 10^{21}$

$$\frac{\eta^2}{\rho} = 10^{41}$$
 dynes

Figure 2 $R \lll 1$

where ν is called the kinematic viscosity. It's easier to remember its dimensions for water: $\nu \approx 10^{-2}$ cm²/sec. The ratio is called the Reynolds number and when that number is small the viscous forces dominate. Now there is an easy way, which I didn't realize at first, to see who should be interested in small Reynolds numbers. If you take the viscosity, η and square it and divide by the density, you get a force (Fig. 2). No other dimensions come in at all, η^2/ρ is a force. For water, since $\eta \approx 10^{-2}$ and $\rho \approx 1$, $\eta^2/\rho \approx 10^{-4}$ dynes. That is a force that will tow anything, large or small, with a Reynolds number of order of magnitude 1. In other words, if you want to tow a submarine with Reynolds number 1 (or strictly speaking $1/6\pi$ if it's a spherical submarine) tow it with 10^{-4} dyne in water. So it's clear in this case that you're interested in small Reynolds number if you're interested in *small forces* in an absolute sense. The only other people who are interested in low Reynolds numbers, although they usually don't have to invoke it, are the geophysicists. The Earth's mantle is supposed to have a viscosity of 10^{21} P. If you now work out η^2/ρ , the force is 10^{41} dyne. That is more than 10^9 times the gravitational force that half the Earth exerts on the other half! So the conclusion is, of course, that in the flow of the mantle of the Earth the Reynolds number is very small indeed.

Now

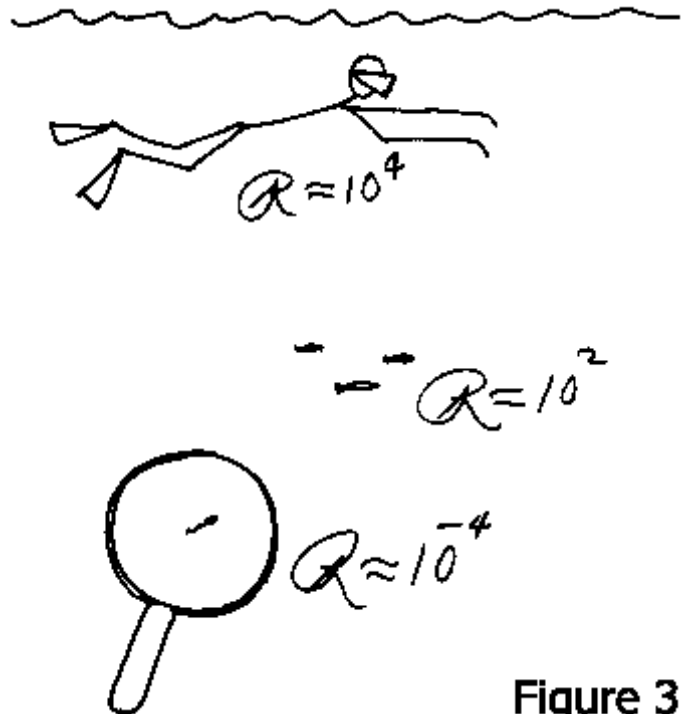
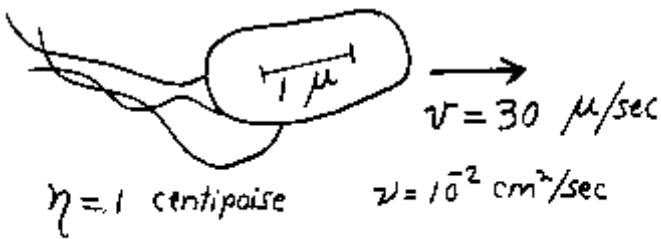


Figure 3

consider things that move through a liquid (Fig. 3). The Reynolds number for a man swimming in a liquid might be 10^4 , if we put in reasonable dimensions, for a goldfish or a tiny guppy it might get down to 10^2 . For the animals that we're going to be talking about, as we'll see in a moment it's about 10^{-4} or 10^{-5} . For these animals inertia is totally irrelevant. We know that $F=ma$, but they could scarcely care less. I'll show you a picture of the real animals in a bit but we are going to be taking about objects which are the order of a micron in size (Fig. 4). That's a micron scale, not a suture, in the animal in Fig. 4. In water where the kinematic viscosity is 10^{-2} cm/sec these things move around with a typical speed of 30 micron/sec. If I have to push that animal to move it, and suddenly I stop pushing, how far will it coast before it slows down? The answer is, about 0.1 angstrom. And it takes



$\eta = 1 \text{ centipoise}$ $\nu = 10^{-2} \text{ cm}^2/\text{sec}$

$R = 3 \times 10^{-5}$

} coasting distance $\approx 0.1 \text{ \AA}$
 } coasting time $\approx 0.3 \text{ microsec.}$

Figure 4

it about 0.6 microsec to slow down. I think this makes it clear what low Reynolds number means. Inertial plays no role whatsoever. If you are at very low Reynolds number, what you are doing at the moment is entirely determined by the forces that are exerted on you at that moment, and by nothing in the past.

It helps to imagine under what conditions a man would be swimming at, say, the same Reynolds number as his own sperm. Well you put him in a swimming pool that is full of molasses, and the you forbid him to move any part of his body faster than 1 cm/min. Now imagine yourself in that condition; you're under the swimming pool in molasses, and now you can only move like the hands of a clock. If under those ground rules you are able to move a few meters in a couple of weeks, you may qualify as a low Reynolds number swimmer.

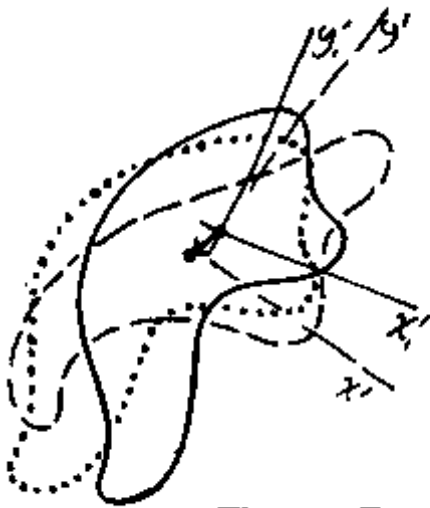
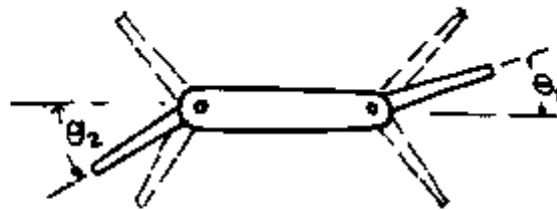


Figure 5



want to talk about swimming at low Reynolds number in a very general way. What does it mean to swim? Well, it means simply that you are in some liquid and are allowed to deform your body in some manner. That's all you can do. Move it around and move it back. Of course, you choose some kind of cyclic deformation because you want to keep swimming, and it doesn't do any good to use a motion that goes to zero asymptotically. You have to keep moving. So, in general, we are interested n cyclic deformations of a body on which there are no external torques or forces except those exerted by the surrounding fluid. In Fig. 5, there is an object which has a shape shown by the solid line; it changes its shape to the dashed contour and then it changes back. When it finally gets back to its original shape, the dotted contour, it has moved over and rotated a little. It has been swimming. When it executed the cycle, a displacement resulted. If it repeats the cycle, it will, of course, effect the same displacement, and in tow dimensions we'd see it progressing around a circle. In three dimensions its most general trajectory is a helix consisting of little kinks, each of which is the result of one cycle of shape change.

Navier - Stokes:

$$-\nabla p + \eta \nabla^2 \vec{v} = \rho \frac{\partial \vec{v}}{\partial t} + \rho (\vec{v} \cdot \nabla) \vec{v}$$

If $Q \ll 1$:

Time doesn't matter. The pattern of motion is the same, whether slow or fast, whether forward or backward in time.

The Scallop Theorem

Figure 6



There is a very funny thing about motion at low Reynolds number, which is the following. One special kind of swimming motion is what I call a reciprocal motion. That is to say, I change my body into a certain shape and then I go back to the original shape by going through the sequence in reverse. At low Reynolds number, everything reverses just fine. Time, in fact, makes no difference---only configuration. If I change quickly or slowly, the pattern of motion is exactly the same. If you take the Navier-Stokes equation and throw away the inertia terms, all you have left is $\nabla^2 v = p/\eta$, where p is the pressure (Fig. 6). So, if the animal tries to swim by a reciprocal motion, it can't go anywhere. Fast or slow, it exactly retraces its trajectory and it's back where it started. A good example of that is a scallop. You know, a scallop opens its shell slowly and closes its shell fast, squirting out water. The moral of this is that the scallop at low Reynolds number is no good. It can't

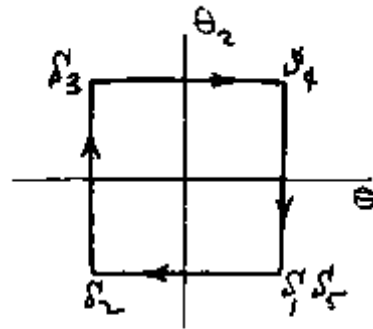


Figure 7

swim because it only has one hinge, and if you have only one degree of freedom in configuration space, you are bound to make a reciprocal motion. There is nothing else you can do. The simplest animal that can swim that way is an animal two hinges. I don't know whether one exists but Fig. 7 shows a hypothetical one. This

animal is like a boat with a rudder at both front and back, and nothing else. This animal can swim. All it has to do is go through the sequence to configurations shown, returning to the original one at S_5 . Its configuration space, of course, is two dimensional with coordinates θ_1, θ_2 . The animal is going around a loop in that configuration space, and that enables it to swim. In fact, I worked this one out just for fun and you can prove from symmetry that it goes along the direction shown in the figure. As an exercise for the student, what is it that distinguishes that direction?

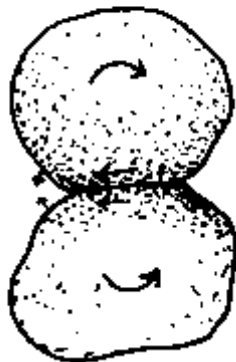


Figure 8

You can invent other animals that have no trouble swimming. We had better be able to invent them, since we know they exist. One you might think of first as a physicist, is a torus. I don't know whether there is a toroidal animal, but whatever other physiological problems it might face, it clearly could swim at low Reynolds number (Fig. 8). Another animal might consist of two cells which were stuck together and were able to roll on one another by having some kind of attraction here while releasing there. That thing will "roll" along. I described it once as a combination caterpillar tractor and bicycle built for two, but that isn't the way it really works. In the animal kingdom, there are at least two other more common solutions to the problem of swimming at low Reynolds number (Fig. 9). One might be called the flexible oar. You see, you can't row a boat at low Reynolds number in molasses--if you are submerged--because the stiff oars are just reciprocating things. But if the oar is flexible, that's not true, because then the oar bends one way during the first half of the stroke and the other during the second half. That's sufficient to elude the theorem that got the scallop. Another method, and the one we'll mainly be talking about, is what I call a corkscrew. If you keep turning it, that, of course, is not a reciprocal change in configuration space and that will propel you. At this point, I wish I could persuade you that the direction in which this helical drive will move is not obvious. Put yourself back in that swimming pool

The flexible oar



The corkscrew

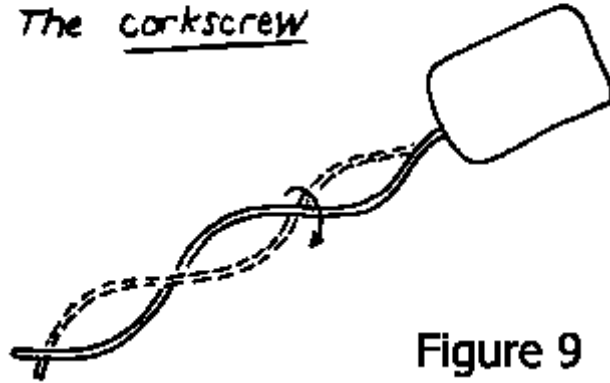
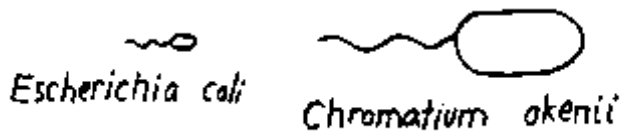


Figure 9

under molasses and move around very, very slowly. Your intuitions about pushing water backwards are irrelevant. That's not what counts. Now, unfortunately, it turns out that the thing does move the way your naive, untutored, and actually incorrect argument would indicate, but that's just a pedagogical misfortune we are always running into.

Well, let's look at some real animals (Fig. 10). This figure I've taken from a paper of Howard Berg that he sent me. Here are three real swimmers. The one we're going to be talking about most is the famous animal, *Escherichia coli*, at A, which is a very tiny thing. Then there are two larger animals. I've copied down their Latin names and the may be old friends to some of you here. This thing (*S. volutans*) swims by waving its body as well as its tail and roughly speaking, a spiral wave runs down that tail. The bacterium *E. coli* on the left is about 2 micron long. The tail is the part that we are interested in. That's the flagellum. Some *E. coli* cells have them coming out the sides; and they may have several, but when they have several they tend to bundle together. Some cells are nonmotile and don't have flagella.



10 μm

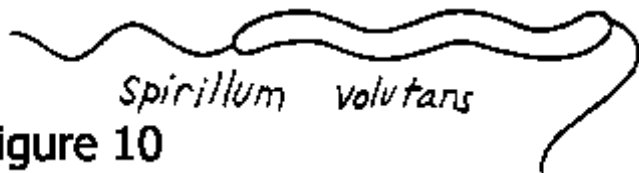


Figure 10

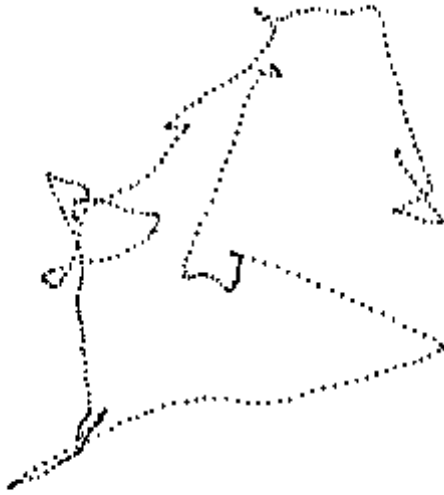


Figure 11

50 μm

To come now to modern times, I want to show a picture of these animals swimming or tracking. This is the work of Howard Berg, and I'll first describe what he did. He started building the apparatus when he was at Harvard. He was interested in studying not the actual mechanics of swimming at all but a much more interesting question, namely, why these things swim and where they swim. In particular, he wanted to study chemotaxis in *E. coli* --seeing how they behave in gradients of nutrients and things like that. So he built a little machine which would track a single bacterium in x,y,z coordinates--just lock onto it optically and track it. He was able then to track one of these bacteria while it was behaving in its normal manner, possibly subject to the influence of gradients of one thing or another. A great advantage of working with a thing like *E. coli* is that there are so many mutant strains that have been well studied that you can use different mutants for different things. The next picture (Fig. 11) is one of his tracks. It shows a projection on a plane of the track of one bacterium. The little dots are 0.1 sec apart so that it was actually running along one of the legs for a second or two and the speed is typically 20--40 microns/sec. Notice that it swims for a while and then stops and goes off in another direction. We'll see later what that might suggest. A year ago, Howard Berg went out on a limb and wrote a paper in *Nature* in which he argued that, on the basis of available evidence, *E. coli* must

swim by rotating their flagella, not by waving them. Within the year a very elegant, crucial experiment by Silverman and Simon at

UC-San Diego showed that this fact is the case. Their experiment involved a mutant strain of *E. coli* bacteria which don't make flagella at all but only make something called the proximal hook to which the flagella would have been attached. They found that with antihook antibodies they could cause these things to glue together. And once in a while one of the bacteria would have its hook glued to the microscope slide, in which case the whole body rotated at constant angular velocity. And when two hooks glued together, the two bodies counter-rotated, as you would expect. It's a beautiful technique. Howard was ready with his tracker and the next picture (Fig. 12) shows his tracker following the end of one of these tethered *E. coli* cells which is stuck to the microscope

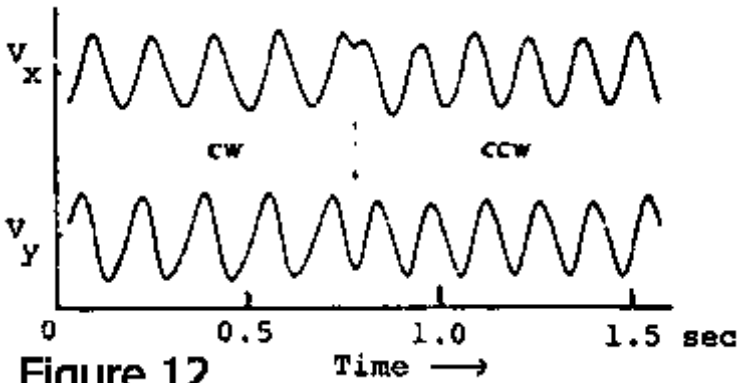
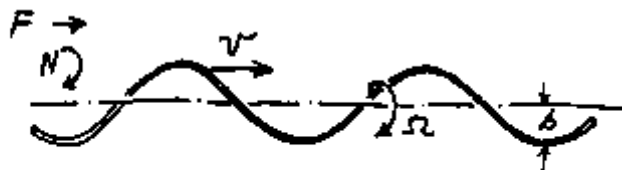


Figure 12

Time \rightarrow

slide by antibody at the place where the flagellum should have been. Plotted here are the two velocity components V_x and V_y . The two velocity components are 90 degrees out of phase. The point being tracked is going in a circle. In the middle of the figure, you see a 90 degrees phase change in one component, a reversal of rotation. They can rotate hundreds of revolutions at constant speed and then turn around and rotate the other way. Evidently the animal actually has a rotary joint, and has a motor inside that's able to drive a flagellum in one direction or the other, a most remarkable piece of machinery.



(force) $F = A v + B \Omega$

(torque) $N = C v + D \Omega$

$$|P| = \begin{vmatrix} A & B \\ C & D \end{vmatrix}$$

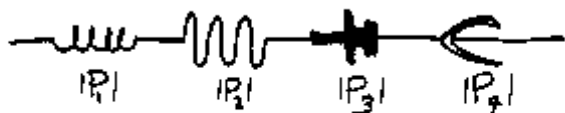
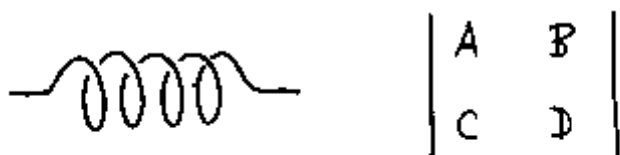


Figure 13 $|P| = |P_1| + |P_2| + |P_3| + |P_4|$

part of this is you can just lick the experimental material off your fingers.



We can prove $C = B$

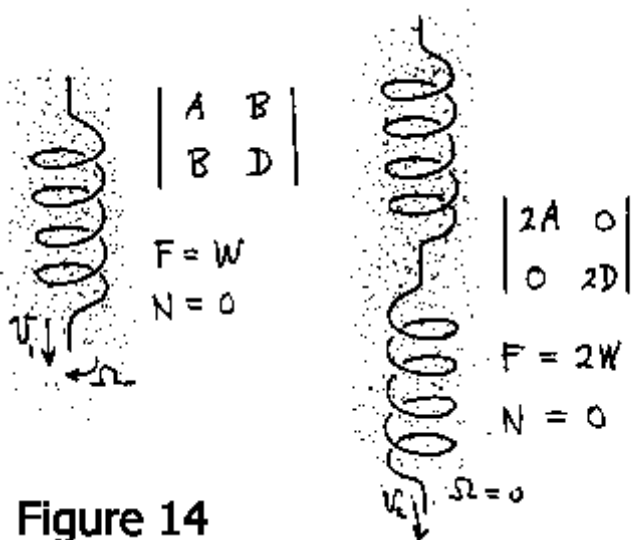


Figure 14

surprise, it was no better at all! I don't really understand that, because the fluid mechanics of these two situations is not at all simple.

I got interested in the way a rotating corkscrew can propel something. Let's consider propulsion in one direction only, parallel to the axis of the helix. The helix can translate and it can rotate; you can apply a force to it and a torque. It has a velocity v and an angular velocity ω . And now remember, at low Reynolds number everything is linear. When everything is linear, you expect to see matrices come in. Force and torque must be related by matrices with constant coefficients, to linear and angular velocity. I call this little 2×2 matrix the propulsion matrix (Fig. 13). If I knew its elements A, B, C, D , I could then find out how good this rotating helix is for propelling anything.

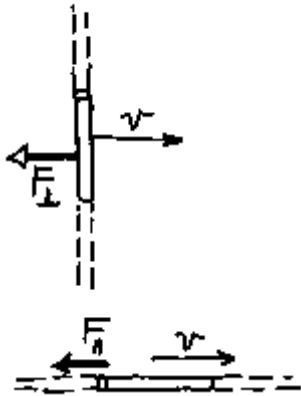
Well, let's try to go on by making some assumptions. If two corkscrews or other devices on the same shaft are far enough from one another so that their velocity patterns don't interact, their propulsive matrices just add. If you allow me that assumption, then there is a very nice way, which I don't have time to explain, of proving that the propulsion matrix must be symmetrical (Fig. 14). So actually the motion is described by only three constants, not four, and they are very easily measured. All you have to do is make a model of this thing and drop in a fluid that you are interested in or not, because these constants are independent of that. And so I did that and that's my one demonstration. I thought this series of talks ought to have one experiment and there it is. We're looking through a tank not of glycerin but of corn syrup, which is cheaper, quite uniform, and has a viscosity of about 50 P or 5000 times the viscosity of water. The nice

Motion at low Reynolds number is very majestic, slow, and regular. You'll notice that the model is actually rotating but rather little. If that were a corkscrew moving through a cork of course, the pattern in projection wouldn't change. It's very very far from that, it's *slipping*, so that it sinks by several wavelengths while it's turning around once. If the matrix were diagonal, the thing would not rotate at all. So all you have to do is just see how much it turns as it sinks and you have got a handle on the off-diagonal element. A nice way to determine the other elements is to run two of these animals, one of which is a spiral and the other is two spirals, in series, of opposite handedness. The matrices add and with two spirals of opposite handedness, the propulsions matrix must be diagonal (Fig. 14). That's not going to rotate; it better not.

The propulsive efficiency is more or less proportional to the square of the off-diagonal element of the matrix. The off-diagonal element depends on the difference between the drag on a wire moving perpendicular to its length and the drag on a wire moving parallel to its length (Fig. 15). These are supposed to differ in a certain limit by a factor of 2. But for the models I've tested that factor is more like 1.5. Since it's that factor minus 1 that counts, that's very bad for efficiency. We thought that if you want something to rotate more while sinking, it would be better not to use a round wire. Something like a slinky ought to be better. I made one and measure its off diagonal elements. Surprise,

Propulsive efficiency $\propto B^2$

$$B \propto \left(\frac{\text{transverse drag}}{\text{longitudinal drag}} - 1 \right)$$

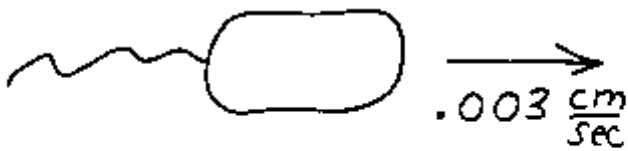


$$\frac{U_1}{U_2} \approx 2$$

Figure 15

In each case there is a logarithmic divergence that you have to worry about, and the two are somewhat different in character. So that theoretical ratio of two I referred to is probably not even right.

When you put all this in and calculate the efficiency, you find that it's really rather low even when the various parameters of the model are optimized. For a sphere which is driven by one of these helical propellers (Fig. 16), I will define the efficiency as the ratio of the work that I would have to do just to putt that thing along to what the man inside it turning the crank has to do. And that turns out to be about 1%. I worried about that result for a while and tried to get Howard interested in it. He didn't pay much attention to it, and he shouldn't have, because it turns out that efficiency is really not the primary problem of the animal's motion. We'll see that when we look at the energy requirement. How much power does it take to run one of these things with a



Energy required, if
 efficiency of propulsion is 1%:

$$2 \times 10^{-8} \text{ erg/sec,}$$

or $\frac{1}{2}$ watt/kilogram

Figure 17

for transport by diffusion, it's l^2 divided by D , the diffusion constant. The ratio of those two times is a measure of the effectiveness of stirring versus that of diffusion for any given distance and diffusion constant.

I'm sure this ratio has someone's name but I don't know the literature and I don't know whose number that's called. Call it S for stirring number, it's just lv/D . You'll notice by the way that the Reynolds number was lv/η , η is the kinematic viscosity in cm^2/sec , and D is the diffusion constant in cm^2/sec , for whatever it is that we are interested in following--let us say a nutrient molecule in water. Now, in every reasonably sized molecules, something like $10^{-5} \text{ cm}^2/\text{sec}$. In the size domain that we're interested in, of micron distances, we find that the stirring number S is 10^{-2} , for the velocities that we are talking about (Fig. 18).

Stirring vs. Diffusion

time for transport by stirring: $\frac{l}{v}$

time for transport by diffusion: $\frac{l^2}{D}$

stirring works if $\frac{lv}{D} > 1$

"S" = $\frac{lv}{D}$
 $\leftarrow 10^{-5} \text{ cm}^2/\text{sec}$

$\left[R = \frac{lv}{\eta} \right]$
 $\leftarrow 10^{-2} \text{ cm}^2/\text{sec}$

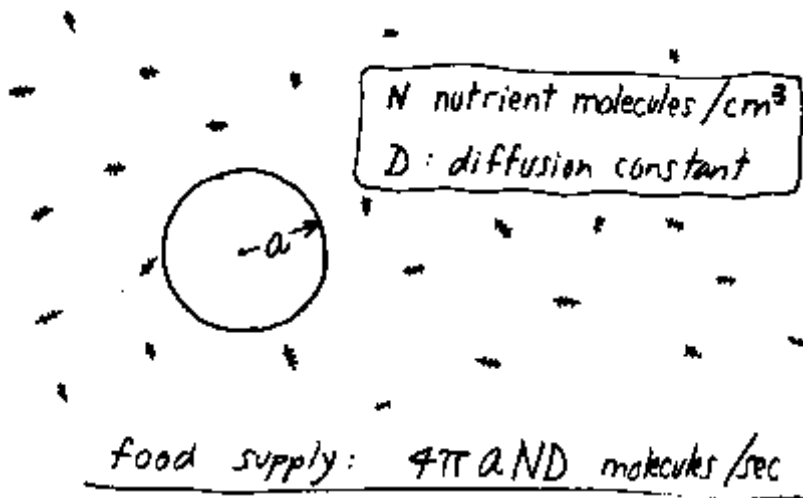


$S \approx 10^{-2}$

local stirring accomplishes nothing

Figure 18

In other words, this bug can't do anything by stirring its local surroundings. It might as well wait for things to diffuse, either in or out. The transport of wastes away from the animal and food to the animal is entirely controlled locally by diffusion. You can thrash around a lot, but the fellow who just sits there quietly waiting for stuff to diffuse will collect just as much.



to increase supply by 10%:

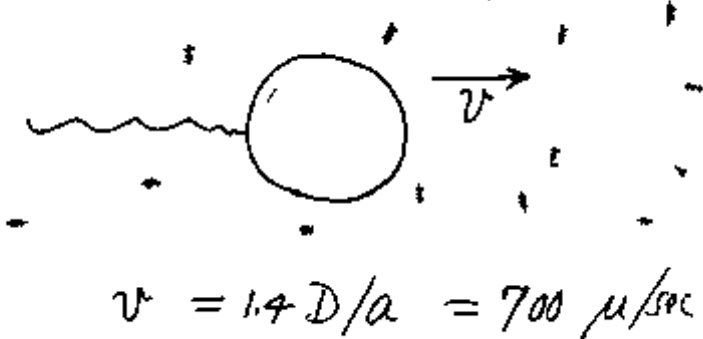
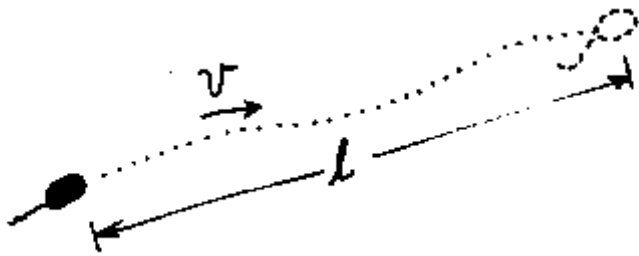


Figure 19

At one time I thought that the reason the thing swims is that if it swims it can get more stuff, because the medium is full of molecules the bug would like to have. All my instincts as a physicist say you should move if you want to scoop that stuff up. You can easily solve the problem of diffusing in the velocity field represented by the Stokes flow around a sphere---for instance, by a relaxation method. I did so and found out how fast the cell would have to go to increase--its food supply. The food supply if it just sits there is $4\pi aND$, where a is the cell's radius (Fig. 19) and N is the concentration of nutrient molecules. to increase its food supply by 10% it would have to move at a speed of 700 microns/sec, which is 20 times as fast as it can swim. The increased intake varies like the square root of the bug's velocity so the swimming does no good at all in that respect. But what it can do is find places where the food is better or more abundant. that is, it does not move like a cow that is grazing a pasture--it moves to find *greener pastures*. And how far does it have to move? Well, it has to move far enough to outrun diffusion. We said before that stirring wouldn't do any good locally, compared to diffusion. But suppose it wants to run over there to see whether there is more over there. Then it must outrun diffusion, and ho do you do that? Well, you go that magic distance, D/v . So the rule is then, to out swim diffusion you have to go a distance which is equal to or greater than this number we had in our S constant. for typical D and v , you have to go about 30 μm and that's just about what the swimming bacteria were doing. If you don't swim that far, you haven't gone anywhere, because it's only on that scale that you could find a difference in your environment with respect to molecules of diffusion constant D (Fig. 20).



to out-swim diffusion:

$$l \geq D/v$$

if $D = 10^{-5} \text{ cm}^2/\text{sec}$, $v = .003 \text{ cm}/\text{sec}$

$$l \geq 30 \mu$$

"If you don't swim that far you haven't gone anywhere."

Figure 20

things are getting worse, don't they change sooner? My suggestion is that there is no point in stopping sooner. there is a sort of bedrock length which outruns diffusion and is useful for sampling the medium. shorter paths would be a ridiculous way to sample. It may be something like that, but as I say, I don't know. the residue of education that I got from this is partly this stuff about simple fluid mechanics, partly the realization that the mechanism of propulsion is really not very important except, of course, for the physiology of that very mysterious motor, which physicists aren't competent even to conjecture about.

I come back for a moment to Osborne Reynolds. That was a very great man. He was a professor of engineering, actually. He was the one who not only invented Reynolds number, but he was also the one who showed what turbulence amounts to and that there is an instability in flow, and all that. He is also the one who solved the problem for how you lubricate a bearing, which is a very subtle problem that I recommend to anyone who hasn't looked into it. But I discovered just recently in reading in his collected works that toward the end of his life, in 1903, he published a very long paper on the details of the *sub mechanical universe*, and he had a complete theory which involved small particles of diameter 10^{-18} cm. It gets very nutty from there on. It's a mechanical model, the particles interact with one another and fill all space. But I thought that, incongruous as it may have seemed to put this kind of stuff in between our studies of the sub mechanical universe today, I believe that Osborne Reynolds would not have found that incongruous, and I'm quite positive that Viki doesn't.

Let's go back and look at one of those sections from Berg's track (Fig. 11). You'll see that there are some little trips, but otherwise you might ask why did it go clear over here and stop. Why did it go back? Well, my suggestion is, and I'd like to put this forward very tentatively, that the reason it does is because it's trying to outrun diffusion. Otherwise, it might as well sit still, as indeed do the mutants who don't have flagella. Now there is still another thing that I put forward with even more hesitation because I haven't tried this out on Howard yet. When he did his chemotaxis experiments, he found a very interesting behavior. If these things are put in a medium where there is a gradient of something that they like, they gradually work their way upstream. But if you look at how they do it and ask what rules they are using, what the algorithm is to use the current language, for finding your way upstream, it turns out that it's very simple. The algorithm is: if things are getting better don't stop so soon. If, in other words, you plot, as Berg has done in some of his papers, the distribution of path lengths between runs and the little stops that he calls "twiddles," the distribution of path lengths if they are going up the gradient gets longer. That's a very simple rule for working your way to where things are better. If they're going down the gradient, though, they don't get shorter. And that seems a little puzzling. Why, if