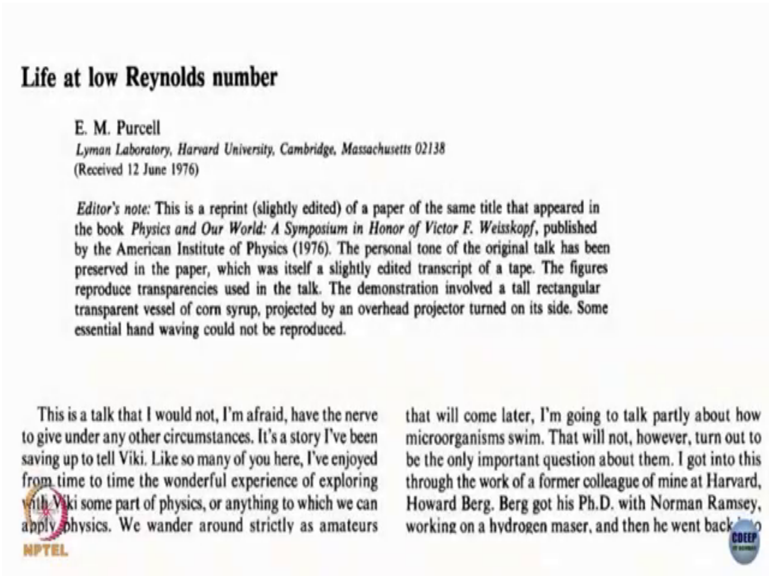
Physics of Biological Systems
Prof. Mithun Mitra
Department of Physics
Indian Institute of Technology, Bombay

Lecture – 21
Bacterial flagellar motion

(Refer Slide Time: 00:17)



Life at low Reynolds number

E. M. Purcell
Lyman Laboratory, Harvard University, Cambridge, Massachusetts 02138
(Received 12 June 1976)

Editor's note: This is a reprint (slightly edited) of a paper of the same title that appeared in the book *Physics and Our World: A Symposium in Honor of Victor F. Weisskopf*, published by the American Institute 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.

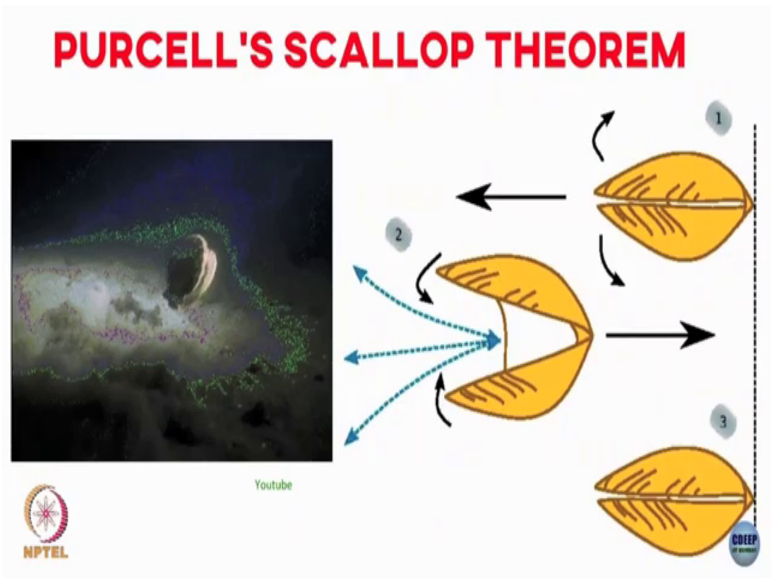
This is a talk that I would not, I'm afraid, have the nerve to give under any other circumstances. It's a story I've been saving up to tell Viki. Like so many of you here, I've enjoyed from time to time the wonderful experience of exploring with Viki some part of physics, or anything to which we can apply physics. We wander around strictly as amateurs 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

It is one of the questions we had asked is that how do what strategies do small organisms like bacteria developed for swimming and how are they different from large scale organisms like fish or humans and so on. So, today we will try to sort of look at this question in a little bit more detail. So, this was one of the first pieces of work was the seminal paper by Purcell life at low Reynolds numbers, this is in the American Journal of Physics. It is actually a talk that he gave in honor of Victor Weisskopf in 1956 and it was then published.

So, it reads like somebody is talking and it is very easy to read and it discusses a lot; so, Purcell had a lot of insight or intuition into how this organisms would behave at these low Reynolds numbers. So, I would encourage all of you to go back and read this paper its one of the seminal works in the field, this and another light paper in 97 which came out in PNAs, again by Purcell.

So, what he asked was this that ok, I want to look at strategies that organisms have evolved. So, let me start by thinking of the simplest possible strategy that I can have the simplest possible organism that I can have and so, what he picked up was this organism called the scallop.

(Refer Slide Time: 01:43)



You may or you know scallops have this nice meat inside which you eat, this one swims. So, what is the scallop has is like two plates like this held together at the hinge and it sort of just moves that hinge back and forth; so, it just moves that hinge back and forth like this. So, it does that at different speeds. So, it opens it up slowly it takes the water comes inside and then it quickly closes it as it closes it push the water gets pushed out, the scallops get pushed forward, ok; so, that is how the scallop cells.

So, what Purcell asked was this that ok, this is a very simple model of how swimming can take place. You have something like this two plates with an angle between them and then you change this angle as a function of time, you open it and close it and as a result you get swimming in the scallop.

So, what he asks is that would this strategy be a successful strategy for swimming, if we are talking about this microorganisms which live in the low Reynolds number. So, at high Reynolds number at high Re this is a successful strategy as is evinced by a scallop this movie does not does not playing, but whatever if it played you would see that the scallop does not need swim.

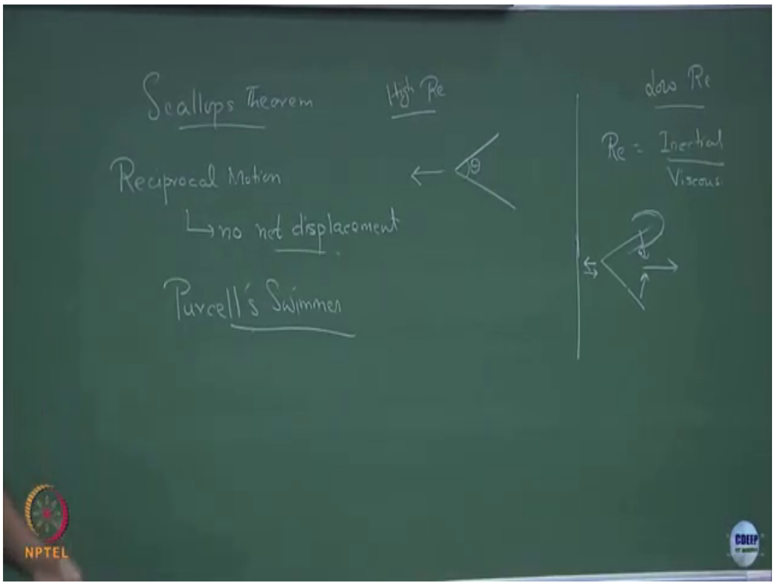
On the other hand if you think about this at low Reynolds numbers; remember, what is at low Reynolds numbers the inertial forces or the kinetic energy. In some sense is quickly dissipated almost instantaneously dissipated by the viscous forces right, that is what we saw last day that the Reynolds number is the inertial by the viscous force skills. And a very low Reynolds number means that there is inertia does not play a role, the viscous forces quickly dissipate whatever kinetic energy that you would have. What that means is that if you were to reproduce this sort of a strategy at low Reynolds number when you are like this and water sort of flows in, ok.

Well, let me do this; the other way let us say you are open and you sort of close it, you expel the water and as a result you move forward a little bit, ok. On the other hand when you open it back up again, you draw back the same amount of water because it is in this highly viscous low Reynolds number medium. You draw back the same amount of water that you are expelled back which means it goes back precisely the same amount that it had moved forward, ok.

So, what Purcell said was this this is called the Purcell scallop theorem that at low Reynolds number whatever amount you move in one direction this given by this arrow, as you as you reverse the motion you are going to move back in the opposite direction by the same amount. So, there is not going to be any net displacement and what this. So, what this scallops theorem says is that if you have any sort of reciprocal motion if you have any sort of reciprocal motion which means that you trace back whatever trajectory you had taken, right.

So, you open it up and precisely by the time reverse trajectory you close it back down in a low Reynolds number world, a motion like that a reciprocal motion will not lead to any this net displacement; so, it will not lead to any net displacement, ok.

(Refer Slide Time: 05:13)

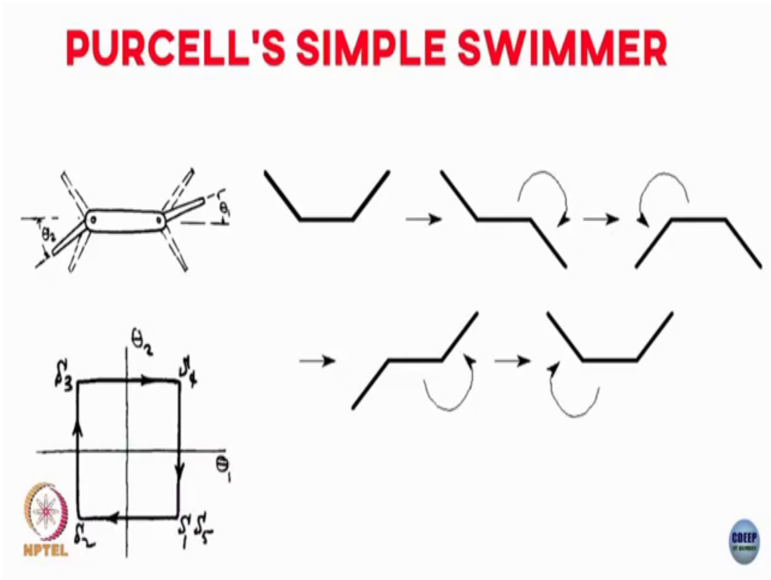


So, then next you ask that well this sort of a strategy will not work, this scallop strategy will not work what do I need in order to have a minimum sort of what do I need at a minimum in order to have a successful strategy for swimming in a world like this in a role when Reynolds number world like this.

And what he said what he came up with this is this fictitious sort of strategy which is called the Purcell swimmer; which is called Purcell swimmer. So, what he said is this that if I have a hinge like this if I have a single hinge then all I can do is some sort of reciprocal motion about this hinge. On the other hand what I need to do is that I need to get back to my original position. So, I am like this lets say I am swimming whatever strategy I used to swim, but ultimately at the end of one swimming stroke I should come back to my original starting position, right.

So, reside is that I need to come back to my original position. So, I need to complete a cycle of these swimming strokes, but without going without retracing back my step and the minimum thing that he came up with to achieve to achieve this object is what is called is this Purcell simple swimmer.

(Refer Slide Time: 06:35)



So, he said that well instead of one hinge, let me imagine an organism which has two arms two arms pivoted on two hinges. So, here is my swimmer, this is the body of the swimmer and I have two arms which can go up and down around these two hinges, ok. So, now, I can imagine that I will complete a complete I will complete a cycle of swimming strokes without going through a reciprocal motion and how do I do that. So, for example, here is my starting position.

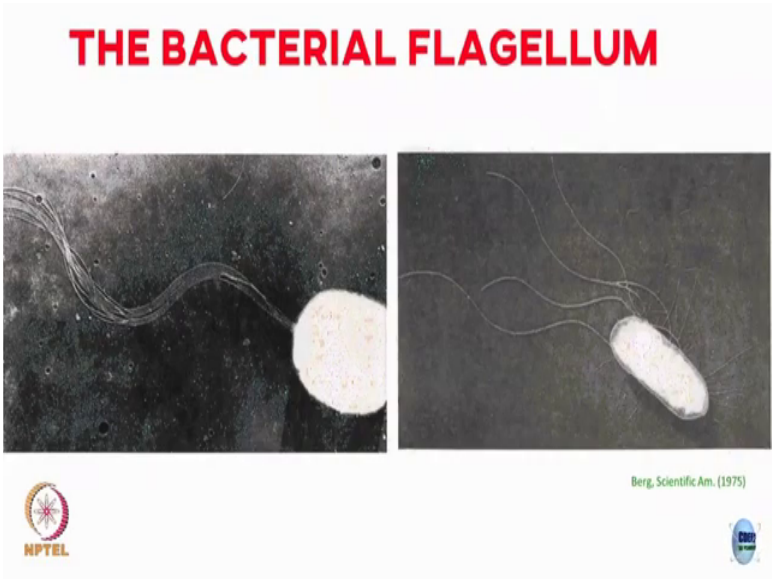
Let us say so, when both arms are up then I put one arm down, I put the other arm down right, I put the other arm down then I put this one up I put that one up, ok. So, at the end of this cycle I have come back to this original position that I started back in, but I have not retraced my trajectory. So, if I want if I this in terms of these angles theta 1 and theta 2 of these two arms that it makes with this body axis.

So, here I am at this stage 1 over there when say theta 1 is positive, theta 2 is negative and I go around in a cycle. So, this is S 1, S 2, S 3, S 4, S 5, ok. So, I go around in this cycle and ultimately I come back to S 5 which is nothing, but the same as S 1 ok. So, I have completed a cycle, but I have not used any reverse motion.

So, I have not reversed back my trajectory and its and what Purcell said was this that if you use a strategy like this where you do not retrace your steps, then it is possible to get net motion as a whole. In this in this sort of a world where you are obeying Stokes equation where you have low Reynolds number physics ok. So, this is what is called Purcell simple swimmer.

So, next you could ask that well this is nice, it is the thought experiment in that what is the simpler swimming strategy that you can come up with, but what strategies have nature evolved in order to swim in this sort of a world. And it turns out that one of the simplest strategies that nature has evolved is to have some sort of a helical motion, and that is easy most prominently seen in as we discussed the bacterial flagellum, right.

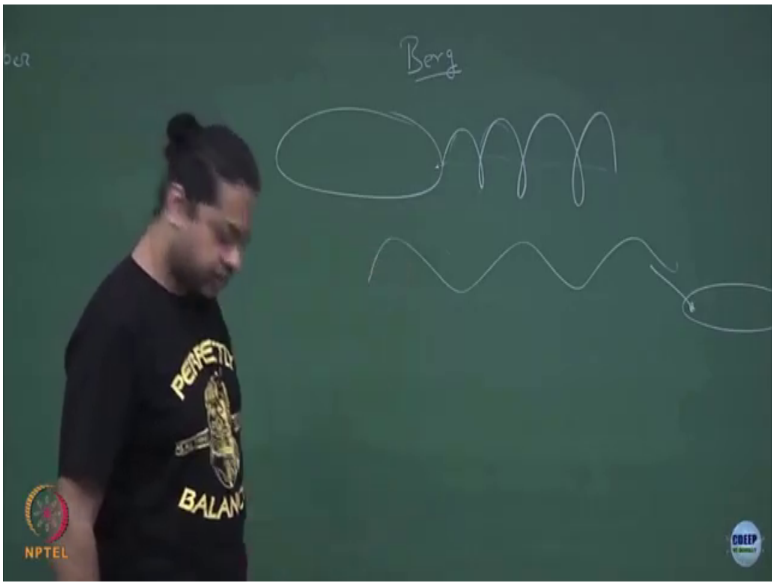
(Refer Slide Time: 08:45)



If you so, just to recap bacteria has these long flagella, it has multiple of these when it wants to move in a given direction. All these flagella bunch up together and they rotate right when they do not want to move these flagella sort of rotate in the opposite direction and they do their own thing. So, this is the bunched up flagella when it rotates this e. coli or this bacterium is going to move in a specific direction in the other case it is not going to move.

So, before it was known what the structure of this flagellum is and how it does what it does; you could think of two options right, you could think that here is my here is my bacterium attacks to this bacterium is a flagella which is say floppy, ok.

(Refer Slide Time: 09:35)

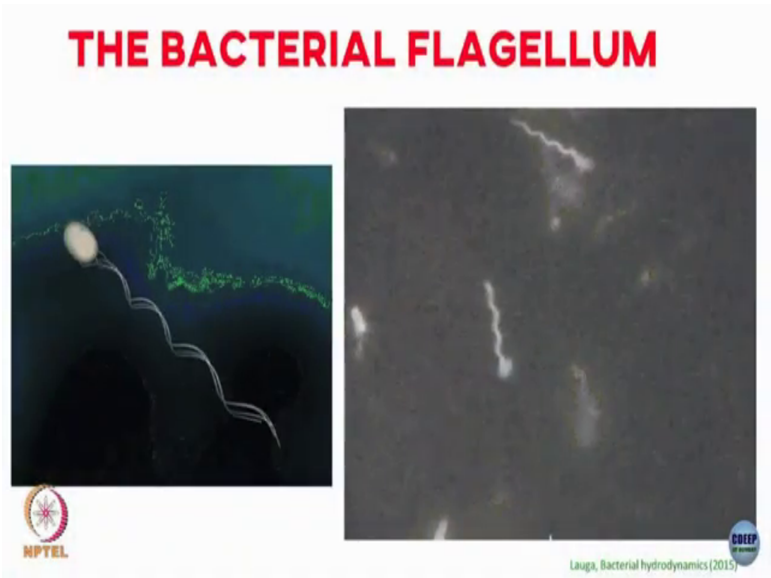


So, it is floppy flagella and I move it I beat it such that I have a helical wave that travels down this flagella length right, that it could be one option or you could have instead of something like this you could have a flagella that was itself helical and you could rotate this helix, right.

You could rotate this helix in order to generate motion and people were not sure which of these were. In fact, people thought that the first scenario was the more likely one because it was thought somewhat inconceivable that you would have this helical structure and then something in the cell would sort of rotate this helical structure and so. So, you would need some sort of a rotary motor which would continuously rotate this flagellum in order to generate this helical waves.

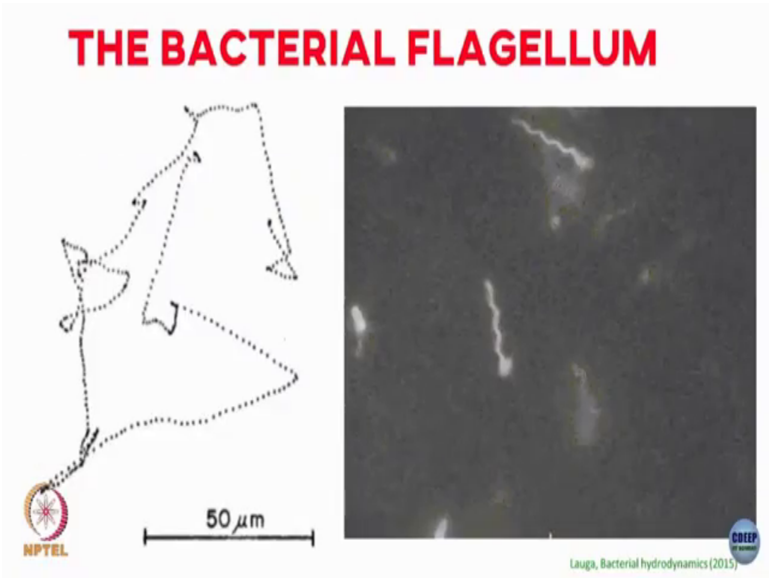
It turns out that is the second option is in fact, the true one and this was shown this was first posited by bird, I do not remember when in the 1980s and so on. And, then later on confirmed by experiments that indeed there is a rotary motor inside the bacterium and this flagella is actually is actually like a helix, the flagella is like a helix and this helix actually rotates in order to generate this motion.

(Refer Slide Time: 10:55)



This is the sort of animation of that you have these helixes which are rotating synchronously and that generates motion. So, here for example, is a trajectory of multiple e. colis which are doing this business. So, you will see they are moving and at some point maybe some will stops over there that one stopped which was when all these flagella became unknotted and they were each doing their own thing. It will do long runs and then occasionally it will stop all this flagella will disengage and will stay there for a bit, ok.

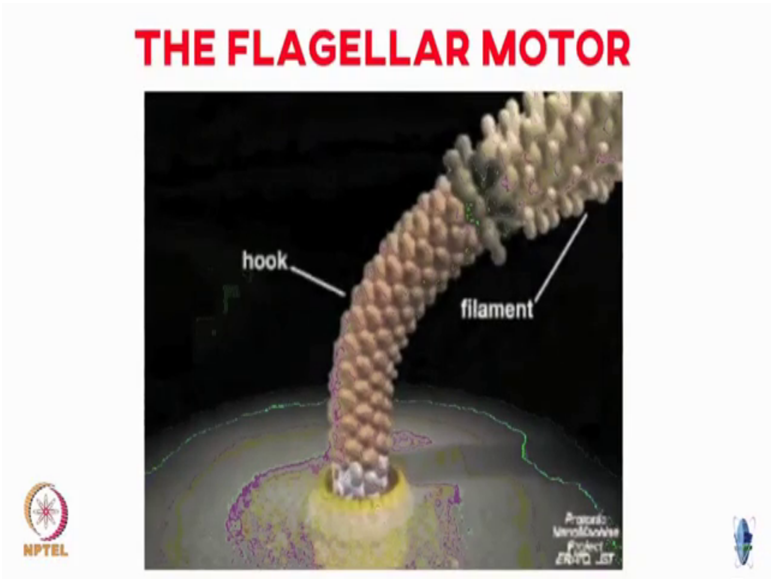
(Refer Slide Time: 11:31)



So, if you look at the trajectories, it looks something like this. So, if you look at this trajectories it will look something like this we will do a long run, then maybe it will stay at some place it will do a what is called a tumble and then again a run and again a tumble and so on. So, this bacterial motion is called this run and tumble motion right, it is called this run and tumble motion; run and tumble motion. So, it runs for some time the flagella beats synchronously and then it stops then again it starts running.

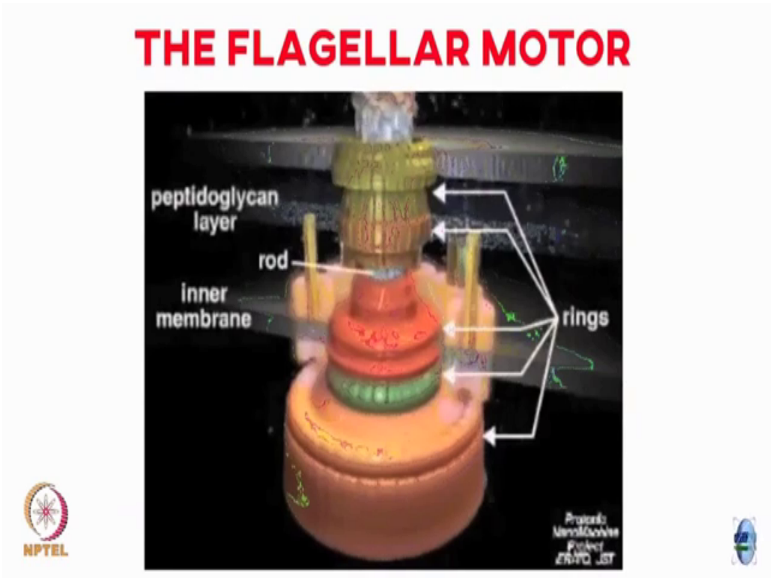
So, what Purcell said is this, that in order to take this sort of a helical flagella and then work out the full hydrodynamic solutions is sort of difficult. So, let me see if I can do something simple and that is that is the argument that I will try to show you today, it is a very nice its very powerful and very beautiful argument.

(Refer Slide Time: 12:45)



So, what he said is this that, ok; so, before I do that I just wanted to show you this flagellar motor. So, this is a flagellum, but so, if you look if you go deep inside and looked at this flagellar it is attached to the cell body through this motor through this bacterial flagellar motor over here. So, there is a filament, this is a hook and through this hook, it is attached to this motor.

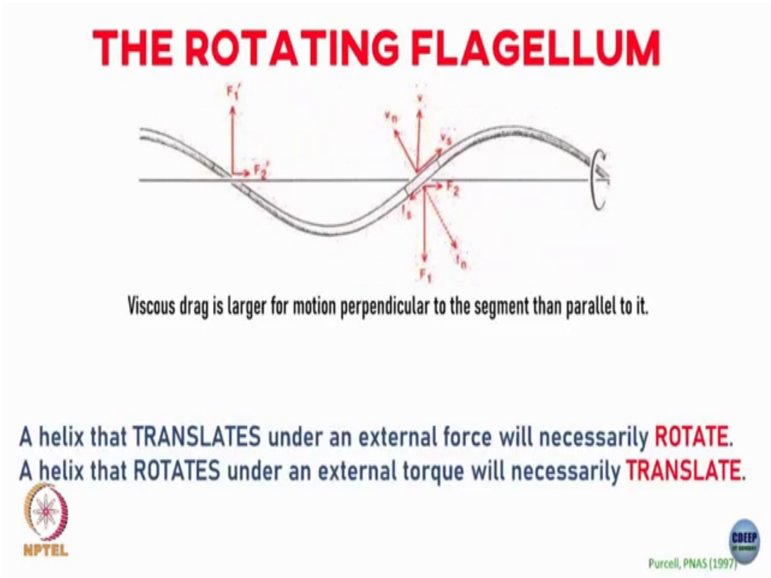
(Refer Slide Time: 12:53)



And this motor actually consumes energy in the form of ATP and it continuously rotates in order to rotate the flagellar, ok. So, it is one of the it is sort of the thing that people see and think about whether evolution can truly have built something, but it indeed has it is a beautiful piece of machinery, it takes this flagella it rotates it and that causes this meeting.

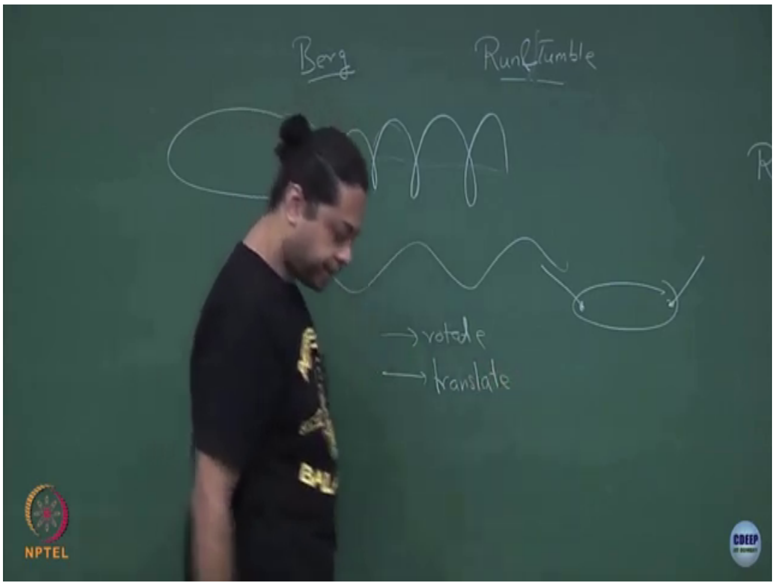
We look at this motor in a little bit more detail when we when you look at molecular motors later on in the course. But I, but the truth is this that there is this helical flagella and there is a motor inside this body, this motor sort of rotates in order to rotate that flagella and then that causes motion, ok.

(Refer Slide Time: 13:45)



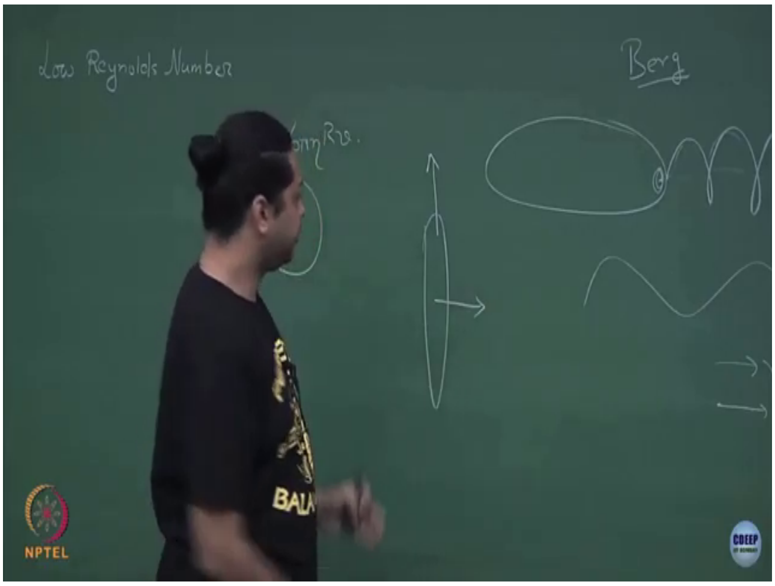
So, here is the argument that if I have a helix and I wrote it; so, what I considered now is a non deformable scaling. So, it cannot would fluctuate its shape and so on, that is not strictly true, but let us assume that. So, it can do only two things it can rotate and it can translate, ok. So, there is the two things that this this idealized helix can do, it can rotate and it can translate.

(Refer Slide Time: 14:07)



Now, if you if you think if you imagine that this sort of an idealized helix and if you rotated this helix, it would necessarily cause some translation, right. If you took a cord screw and you sort of rotated it that would cause some translational motion. On conversely, if you took a course when you translated it that would cause some rotational motion as well and the way to see it in the language of these drag forces and so on, is to see that so, if you think; so, we know what is the drag force for a spherical body which is 6 pi eta Rv, right.

(Refer Slide Time: 14:49)



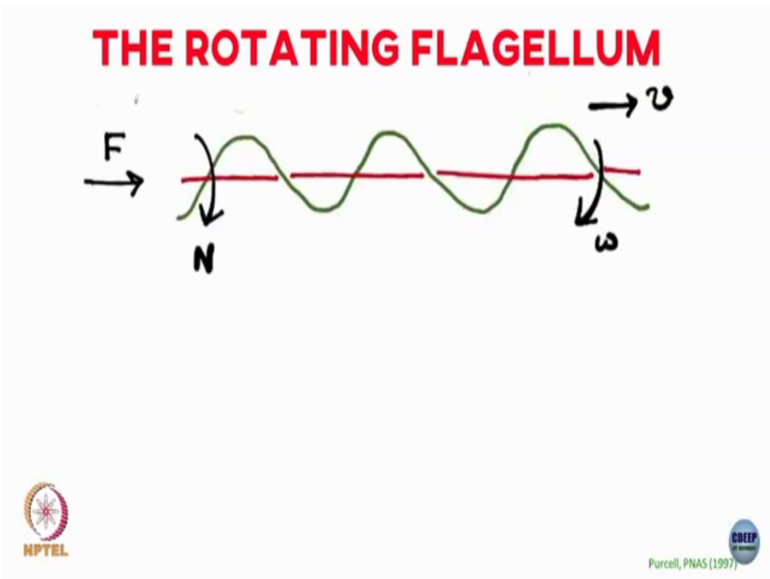
This is a spherically symmetric body on the other hand if I took a non-symmetric body something like this, then I would have a drag coefficient which is different in this direction as opposed to this direction, right. So, if you were moving in in this way you would face some drag viscous back if we were moving like this through a fluid it face a different viscous drag, right.

So, the idea is this that if you think about this helical coil, let us say it is it is moving. So, it has some velocity like that you decompose that velocity into a component which is parallel to this flagella and one which is perpendicular to this flagella, right. Each of these will cause a viscous drag right, F is going to be proportional to the velocity, but this the viscous drags will be different because the drag coefficients are different in these two directions along the axis perpendicular to the axis and along the axis. Because, these will be different, you will have a net force you will have a net drag force which is not going to be in the same direction as the velocity that you moved in right,.

And then, if you add up these drag forces from these different segments. So, for example, here are the two sort of whatever this way and that way, I forget the word two pairs in this segment then you will see that the drag you will have a net force which is going to act along the axis of this helix, ok. So, this F 1 and this F 1 prime will sort of cancel this F 2 and this F 2 prime will add up they will point in the same direction and therefore, if you have a sort of rotation that is going to give rise to this sort of this is going to give rise to an sort of force which is going to make this helix move along the axis of the helix, right.

So, this is sort of intuitively obvious, if you rotate a box through its going to move and so on, but you can also think of it in terms of these drag forces. And so, basically whenever you have a helix that translates under an external force it will necessarily rotate, conversely a real except rotates under an external torque will necessarily translate. So, this was Purcell starting point, all right.

(Refer Slide Time: 16:59)



So, here is my here is my flagellum here is my cartoon of the flagellum I can apply a force on it, I can apply F, I can apply a torque on it and as a result it can move translationally with the velocity v, it can rotate with a angular velocity omega, ok. Now, Purcell's cells that well let me try to relate this force and this torque to this angular velocity and this linear velocity. So, I have these two points, v is the force F and the torque N, right.