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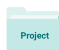
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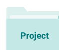
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Reference: *Biol. Bull.* **192:** 137–138. (February, 1997)

Discussion

NICK: Is it possible to purify the statoliths?

KISS: Our group and others have tried for some while, but it does seem to be difficult. The problem is that they are almost too dense and there are many technical difficulties.

NICK: If they are so very dense, they should be more easily isolated.

KISS: Yes and no. The density of pure barium sulfate is about 4.5, and it goes through every gradient. We would be more interested in isolating the statoliths with the membrane around them, and that is certainly very difficult because you have this solid rock in a membrane. The membrane is lost somewhere in the gradient. So although I agree with you, there may also be a problem of quantity.

JACOBS: Dr. Kiss, you implied that the statoliths in *Chara* are not active themselves, but just diverting material to the upper side of the cell. Do you think that is the case, and if so, what's the evidence for this as opposed to a more direct effect?

KISS: The model I presented is primarily from the Sievers group. I think that other things are involved besides Golgi vesicles being physically displaced.

QUESTION: Has anyone measured the two sides of the curving rhizoid to see which of them is bowed more than normal?

KISS: There have been detailed studies with beads and particles. It's a bowing rather than a bulging mechanism.

NICK: I have a small contribution to the question of this diversion hypothesis. There's an old paper (unfortunately forgotten because it's written in German) by Friedrich and Hertel (see Nick abstract). They have shown that, when you apply different strengths of acceleration, the curvature goes with the dose even if the sedimentation is already saturated. This speaks against a pure proximity mechanism.

KISS: I would agree with you on that.

ROUX: Have either one of you tried to use RGDS to try to inhibit your gravity responses? [Ed: RGDS is the tetrapeptide Arg-Gly-Asp-Ser contained in the integrin recognition site of many protein ligans (Schwartz *et al.* 1995. *Annu. Rev. Cell. Biol.* **11:** 549–599.)]

KISS: Randy Wayne has done that with the internodal cells (Wayne *et al.* 1992. *J. Cell. Sci.* **101(3):** 611–623). This indicates that the gravireceptor in *Chara* may be an integrin-like protein. The approach that we are trying now is to microinject anti-integrin antibodies into the rhizoid. We have not done the RGDS experiments with the rhizoids.

BARLOW, R.: Dr. Häder, you presented a model indicating that the direction of motion is dependent on the location of channels in the membrane. You placed the channels in one part of the cell so that it would move in one particular direction. It isn't clear to me why you impose that restriction on the model.

HÄDER: The problem in the mechanism of reorientation is that, at a given point in time, the cell swings out its flagellum, which brings the front end over. This has been shown to be the case in both graviorientation and phototaxis. When the cell is swimming on a helical path, it is not only moving conically, it is really rotating, so the flagellum moves all the way around. Whenever you have a light source from one side, and this stimulus hits the cell in the right direction, the flagellum will swing out on the other side and turn the front end stepwise in the direction of the light. By analogy, for graviorientation you need to have the cell in a certain position when it swings out its flagellum. When you have the channels all the way around, some channels would be activated all the time. This would be independent of whether the cells are swimming horizontally, downwards, or upwards. So we assume that the channels are in a certain position, and the cell aims for minimal modulation of the signal. This occurs when the channels are at the top. When the cell is swimming upwards, the whole pressure goes downwards where there are no channels, or fewer channels. Each time the cell deviates from that course, moving either horizontally or downwards, it will activate the channels. This will then lead to reorientation

of the flagellum, which will bring the cell upwards again.

BARLOW, R.: I can certainly understand why having channels uniformly located all over the cell leads to a problem, but it's not at all clear to me, even with your explanation, why having the channels on one part or the other of the cell would lead to the directionality you observe. It seems to me that you could develop a workable model with channels at either pole of the cell. Am I missing something important?

HÄDER: We did that by running a model. When the channels are at either pole, the cells would go up or down equally well. That might explain the crossover that is observed between the young and the old cells. One thing that we cannot distinguish in that model is whether the channels are distributed symmetrically round the top of the cell, or whether they are oriented only on the same side as the flagellum.

QUESTION: How did you rule out the presence of channels in the flagella?

HÄDER: The flagellum moves with a frequency of 50 Hz in this flagellate, and it will be in various positions; so the flagellum is not a good choice for positioning the channels. One possibility is that the front end of the cell has an invagination, referred to as a reservoir. The flagellum doesn't sit on the tip of the flagellate, but rather inside the reservoir. This reservoir does not have the pellicule, which consists of proteinaceous strips going round the cell, and could be a candidate for the location of the channels.

QUESTION: Did you look at the effect of the RGDS peptide on your cells?

HÄDER: We did not try this peptide with *Euglena.*

QUESTION: Dr. Kiss, did you try any buoyancy experiments with the rhizoid?

KISS: No, these were done with internodal cells by Randy Wayne and his colleagues (in the *Chara* internode).

MORRIS: Dr. Häder, I have a question about your experiments with Ficoll. Presumably this is also going to have an osmotic effect. Do you know the general effects of the osmotic perturbation? Also, can you just take the flagella off these *Euglena?* If so, what happens to the cells, do they just sink? I wondered if you could address the problem of using gadolinium, because it also blocks calcium channels, and that is going to have enormous effects on motility and so on. Finally, have you tried any other inhibitors to block the mechanoresponses?

HÄDER: In answer to your first question, the Ficoll we were using has a molecular weight of 400,000. We checked osmotic effects with Ficolls of lower molecular weight and could find no effect on graviorientation. As I mentioned, we did all the experiments with phototaxis and gravitaxis in parallel. Another potential concern to us was that Ficoll was also changing the viscosity of the medium. As a control for this, we used methyl cellulose, which has much higher viscosity. Our concern was that there could be a disturbance of the timing in an organism that rotates, where it might take a certain time between the application of a stimulus and the response. During this time, the flagellum could be one quarter or half way round the cell. However, when we used higher concentrations of methyl cellulose in an attempt to decrease the velocity of this movement, we saw no effect. In answer to the next question, we can distinguish very easily between effects on motility or swimming velocity and on orientation. Even when the cells are swimming very slowly, we can determine whether they are moving up or down. Thus we can distinguish whether we are affecting graviperception or anything in the cellular metabolism that could slow the cell down. As long as the cells are swimming in a specific direction, we can detect this.

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