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A down to earth model of gravisensing or Newton's Law of Gravitation from the apple's perspective

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Abbreviations – ECM, extracellular matrix; RGDS, tetrapeptide Arg-Gly-Asp-Ser; YIGSR, oligopeptide Tyr-Ile-Gly-Ser-Arg.

We could call Isaac Newton an honorary botanist since the apple tree may have played a noble role in his formulation of the Law of Gravitation that describes how planets, the moon, balls on an inclined plane and apples respond to gravity (Brewster 1965, de Villamil 1931, Gjertsen 1986, McKie and de Beer 1951/1952, Rattansi 1974). We will discuss Newton's Law of Gravitation from the apple's perspective.

It is fascinating to consider the mechanisms involved in the perception of gravity in living organisms since the force of gravity is the weakest of the fundamental forces. Yet because of its constancy, it influences many biological processes. For example, gravity is responsible for directing the growth of a seedling. The cells of the seedling sense gravity so that the root grows down and the shoot grows up. Likewise, gravity effects the orientation of animals. Look around, everyone in the room is sitting with their head up and their feet down. Although partially due to politeness, it is mainly a consequence of the ability of our cells to sense gravity (Feynman 1985).

Sedimenting conglomerates of sand, known as statoliths, are involved in the uprighting response of crustaceans (Prentiss 1901). For example, when a horseshoe crab or a lobster is tilted, the heavy mass falls on a number of hair cells, compressing the extracellular matrix (ECM)-plasma membrane junction of those cells and relieving the compression on the hair cells on the other side of the statocyst. The cells that experience an increased compression increase the frequency of the electrical signal they transmit to the brain. This causes the animal to right itself. Once the animal is upright again, there is no differential pressure on the hairs of one side compared with the other and the uprighting response is terminated.

Bertold (1886) and Noll (1892) suggested that plants may sense gravity in a manner similar to that of crustaceans, and Nemec (1900), who studied the gravitropism of roots, observed that sedimenting starch grains were prevalent in root cap cells. Moreover, he found that the roots did not bend in response to gravity after the root cap was removed. Similar surgical experiments were done by Haberlandt (1900) with shoots. From these experiments, Nemec and Haberlandt independently concluded that starch grains were the gravisensor in plants, named them statoliths and enunciated what has come to be the starch-statolith or classical theory of gravity sensing (Darwin 1903, 1904).

Originally it was believed that the statoliths had to fall to the bottom of the cell to effect the response (Hawker

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1932). In order to act as a mechanical signal, a sedimenting statolith must transmit energy to a gravireceptor and the kinetic or potential energy must be greater than the energy of thermal noise (≈kT, where k is Boltzmann's constant and T is the absolute temperature). How much energy is there in a falling statolith? Given the difference between the density of the amyloplast (ρ = 1 500 kg m^{-3}) and the density of the cytoplasm (ρ = 1 014 kg m^{-3}), the volume of an amyloplast (V = 1.9×10^{-17} m^3) and the velocity of falling amyloplasts (v = 3.3×10^{-7} m s^{-1}; Sack et al. 1985), the kinetic energy (KE = $mv^2/2$, where m = $(\Delta\rho)$V) of a falling statolith would be only 5×10^{-28} J or 0.0000001 kT; too low to be recognized as a signal among molecular energies or states caused by thermal noise.

On the other hand, the potential energy (PE = Fd, where F = mg) of an amyloplast falling a distance (d) of just 100 nanometers would be 9×10^{-21} J, or approximately twice as large as thermal noise. The greater the sedimentation distance, the greater the quantity of energy available to do work. Thus it would be possible for a falling amyloplast to function as a statolith by transferring its potential energy to a receptor. By which mechanism would it transfer its potential energy? Sievers et al. (1995) proposed that the falling amyloplasts would pull on actin microfilaments which in turn would activate a receptor in the plasma membrane or cortical ER. However, while there is evidence that cytochalasin D disturbs the polarity of cells involved in the sensing of gravity (Hilaire et al. 1995), increases the sedimentation velocity of plastids (Sievers et al. 1989) and affects the membrane potentials in gravistimulated roots (Sievers et al. 1995), cytochalasin D has no effect on gravitropism (M. P. Staves, R. Wayne and A. C. Leopold, unpublished data), indicating that microfilaments are not involved in transmitting the potential energy of falling amyloplasts.

Another fly in the ointment for the statolith-microfilaments theory of gravisensing comes from the observation that mutants that lack starch in their plastids still respond to gravity, although with a reduced sensitivity (Casper and Pickard 1989, Kiss et al. 1989, Sack 1991). In the cells of these mutants, the starchless plastids are smaller, less dense and sediment imperceptively at 1 *g*. Thus the potential energy available to activate a receptor will be lower than in the wild type. Thus the proposal that the potential energy made available to do work by the sedimentation of plastids is necessary to activate the gravireceptor should not be accepted without reservation.

The evidence underlying the pronouncement of the classical statolith theory rested on the correlation between the presence of sedimenting starch grains and the ability of an organ to respond to gravity. However, there are other gravity responses, such as the gravitropic responses of *Phycomyces* and *Physcomitrella*, the differentiation of vascular tissue and the polarity of cytoplasmic streaming in characean internodal cells where the ability to respond to gravity is not correlated with the presence of sedimenting statoliths (Gersani and Sachs 1990, Sack 1991). It is possible that the plasma membrane acts as the gravireceptor in these cells and the settling of the mass of the whole protoplast is important for the realization of graviresponse, as suggested by Czapek (1898). Is it possible that the plasma membrane acts as the gravireceptor in all cells and the starch grains function merely as ballast to make the cell more sensitive to gravity? We would like to describe to you the experiments that led us to the conclusion that the protoplast as a whole settles in response to gravity, and that the gravireceptor is present in the plasma membrane-ECM junction.

Ewart (1903) discovered that gravity induces a polarity of cytoplasmic streaming in the internodal cells of *Chara*, and this observation has been extended to other species (Bottelier 1934, Buchen et al. 1991, Hayashi 1957, Hejnowicz et al. 1985). We use the gravity-induced polarity of cytoplasmic streaming solely as a rapid, noninvasive assay to determine the cell's ability to sense gravity. We consider that the cell has sensed gravity in a normal manner when the velocity of the downwardly-directed stream is greater than the velocity of the upwardly directed stream. When there is no difference in velocity, we consider that the cell was not able to sense gravity, and when the velocity of the upwardly-directed stream is greater than the velocity of the downwardly-directed stream, we consider that the cell has a reversed response to gravity (Wayne et al. 1990).

Nemec localized the site of graviperception in roots with amputation experiments, and we amputated the ends of the internodal cell to localize the gravireceptor. We found that both ends are required for characean internodal cells to sense gravity (Wayne et al. 1990). While UV irradiation has no effect when applied to the middle of the cell, the ability to sense gravity is lost when either end of the cell is irradiated. Thus we considered that the gravireceptors were localized at the ends of the cell. We modeled the cell as a water-filled balloon inside a cardboard box and proposed that the cell determined "down" as the end where there was an increase in the compression of the plasma membrane against the ECM and "up" as the end where there was a relief of compression, or a tension if the plasma membrane were attached to the ECM. In order to test this hypothesis, we bathed the cell in low osmotic media of varying densities and found that when the density of the protoplast was greater than the density of the medium, the cell had a normal response to gravity. When the density of the protoplast was equal to the density of the medium, the cell had no response to gravity, and when the density of the protoplast was less than the density of the medium, the cell had a reversed response to gravity. Thus we concluded that the cell did not perceive up and down per se, but actually sensed the tension and compression at the plasma membrane-ECM junction that was caused by the gravitational pressure.

If this postulate be true, we should be able to induce a polarity in cytoplasmic streaming by applying a unidi-

rectional force at one end of a horizontal cell. Indeed, the application of hydrostatic pressure, which caused a unidirectional force, induced a polarity in cytoplasmic streaming such that the velocity of cytoplasmic streaming was always greater away from the site of tension, and slower away from the site of compression (Staves et al. 1992). Moreover, as in gravity sensing, the internodal cells were unable to sense the unidirectional force if their ends were removed or irradiated with UV light. In addition, application of a force in a direction opposite the force of gravity nullifies the graviresponse, and if the unidirectionally applied hydrostatic force is large enough, it reverses the polarity of cytoplasmic streaming in vertical cells. Thus a unidirectionally applied hydrostatic pressure mimics gravity in inducing a polarity of cytoplasmic streaming in characean internodal cells. These results add weight to the conclusion that cells sense gravity by sensing tension and compression, not up and down.

We used impermeant hydrolytic enzymes to try to probe the nature of the molecules that sense tension and compression at the plasma membrane-ECM junction. We found that cellulysin, a mixture of many hydrolytic enzymes, including glucanases and proteases, inhibits gravisensing in characean internodal cells. Then we set out to test the effect of more specific enzymes on gravity sensing. We concluded from these experiments that cellulose, hemicellulose and proteins are involved in gravisensing (Wayne et al. 1992). Moreover, we found that the tetrapeptide Arg-Gly-Asp-Ser (RGDS) specifically inhibited gravity sensing, indicating that an integrin-like protein may be the gravireceptor. RGDS, like the hydrolytic enzymes discussed above, is only effective in inhibiting gravisensing when it is applied to the ends of the cell.

In fact, we have found that RGDS only inhibits gravity sensing when it is applied to the top of the cell, when the density of the protoplast is greater than the density of the external medium, and when it is applied to the bottom of the cell when the density of the protoplast is less than the density of the external medium. This means that RGDS inhibits gravity sensing when and only when it is applied to the end of the cell that experiences tension, and RGDS is a specific inhibitor of the tension receptor.

Thus we set out to find a peptide or enzyme that would specifically inhibit the compression receptor. We found that the oligopeptide Tyr-Ile-Gly-Ser-Arg (YIGSR; a fragment of laminin, a protein that occurs in some extracellular matrices) inhibits gravity sensing when it is applied to the bottom of the cell, when the density of the protoplast is greater than the density of the external medium, and when it is applied to the top of the cell when the density of the protoplast is less than the density of the external medium. This means that YIGSR inhibits gravity sensing when and only when it is applied to the end of the cell that experiences compression, and YIGSR is a specific inhibitor of the compression receptor (M. P. Staves et al. unpublished data). Interestingly, when RGDS is applied to the site of compression and YIGSR is applied to the site of tension, the cell responds normally to gravity. However, when the cell is inverted, so that the RGDS is at the site of tension and the YIGSR is at the site of compression, the cell no longer responds to gravity. Thus we can distinguish the functional tension receptor from the functional compression receptor by its ability to bind these peptides. At present, we do not know whether the two activites are present on one and the same protein or on separate proteins.

It is natural to ask the question whether or not the tension and compression caused by the falling of the protoplast provides enough energy for these putative receptors to initiate a signal transduction sequence that would lead to the observed response. How much is enough energy? Taking a thermodynamic approach, we could say that the energy of thermal noise ($\approx kT$) will serve as an absolute minimal estimate. However, we can also take a comparative biological approach which may provide a more realistic approach to relate energy to information. Using the reasoning of Leo Szilard (1964), who solved the problem of Maxwell's Demon, we can say that an increase in entropy is equivalent to the release of information. Let's consider a cell with a plasma membrane that separates the protoplasmic space from the external space. Since the $[Ca^{2+}]$ in the extracellular space is 10^{-2} mol m^{-3}, approximately one hundred times greater than the intracellular concentration of Ca^{2+}, the entropy, in terms of Ca^{2+} is low. So if a stimulus were to cause a change in $[Ca^{2+}]_i$ from 10^{-4} to 10^{-3} mol m^{-3}, the entropy would increase, and information would become available. A change in $[Ca^{2+}]_i$ from 10^{-4} to 10^{-3} mol m^{-3} is sufficient to provide information to a wide variey of cells such as (1) muscle cells to cause them to contract in response to electrical stimulation, (2) nerve or characean internodal cells to cause them to generate an action potential in response to electrical stimulation, and (3) aleurone cells to secrete α amylase in response to gibberellic acid. Thus we can conclude that changing $[Ca^{2+}]_i$ from 10^{-4} to 10^{-3} mol m^{-3} provides a sufficient increase in entropy to act as the "biological quantum of information" (Wayne et al. 1990).

The potential energy made available to do work when the entire protoplast of *Chara* falls 10^{-9} m (enough to compress or stretch an average protein by about 10–20%) is approximately 6×10^{-16} J. This is obtained by assuming that the length of a cylindrical cell is 10^{-2} m, the diameter is 5×10^{-4} m, the density of the protoplast (as measured gravimetrically) is 1 015 kg m^{-3} (Staves et al. 1996) and the density of the medium is 1 000 kg m^{-3}. This is about 10^5 times greater than the energy of thermal noise and could activate 7 500 mechanosensitive channels that have an energy requirement similar to that found in hair cells (8×10^{-20} J; Howard et al. 1988). Based on energetics, directionality, adaptation kinetics, and inhibitor specificity, we have concluded that the mechanosensitive Ca^{2+} channels involved in gravisensing are likely to be displacement sensitive channels such

as those found in hair cells, and not stretch-activated channels (Staves and Wayne 1993). If the mechanosensitive channels pass 5×10^6 Ca^{2+} s^{-1}, then 3.8×10^{10} Ca^{2+} ($= 6 \times 10^{-14}$ mol) would enter the cell per second. If the cytoplasmic space occupied 5% of the cellular volume, it would take 3.5×10^{-13} mol of Ca^{2+} to raise $[Ca^{2+}]_i$ from 10^{-4} to 10^{-3} mol m^{-3}, and this would take approximately 6 s. Thus the potential energy made available to do work by the falling of the protoplast would supply sufficient energy to be biologically informative.

Ca^{2+} is required for the graviresponse in *Chara* and treating the cells with the organic Ca^{2+} channel blockers, nifedipine, verapamil and ω-conotoxin, inhibits the ability of the cells to respond to gravity. These drugs only inhibit gravity sensing when they are applied to the ends of the cell. Thus the flux of Ca^{2+} across the plasma membrane at the ends of the cell is necessary for the graviresponse. We were interested in measuring the flux of Ca^{2+} across the plasma membrane with an inexpensive, nonradioactive probe. We found that Sr^{2+} can substitute for Ca^{2+} in the gravity response, and thus decided to use Sr^{2+} as a tracer for Ca^{2+}. We have measured the flux of Sr^{2+} into horizontal cells. Again, we find a difference between the ends and the middle of the cell. The flux into the middle of the cell is approximately 10 nmol m^{-2} s^{-1}, while the flux into the ends of the cell is about 20 nmol m^{-2} s^{-1} (M. P. Staves et al. unpublished data).

We found that in vertical cells, the flux of Sr^{2+} increases from 20 to 60 nmol m^{-2} s^{-1} at the end of the cell that experiences tension, while the flux remains unchanged or decreases insignificantly at the end that experiences compression (Staves et al. 1995). The increased flux of Sr^{2+} is inhibited by RGDS. The increased activation at the site of tension results in a polarity in the flux of Sr^{2+}. The consequence of inducing a polarity in the flux of Ca^{2+} is that the velocity away from the site of the higher flux increases, while the velocity away from the site of the lower flux, decreases, resulting in a polarity in the velocity of cytoplasmic streaming.

We have developed the "gravitational pressure model" from the data described above to explain how *Chara* cells sense gravity. But is our model applicable to higher plant cells? The potential energy made available to do work as a consequence of the falling of a tiny (2×10^{-5} m^3) columella protoplast would at first glance be 8×10^{-15} $m^3/3.9 \times 10^{-9}$ $m^3 = 2 \times 10^{-6}$ times smaller than the energy made available by the falling of the protoplast of a *Chara* internodal cell since the volume is so much smaller. This would result in a release of energy of about 10^{-21} J. However, the columella cells, in contrast to characean internodal cells are not mostly vacuolate, but contain dense cytoplasm and even denser amyloplasts. Therefore their density is 1 063 kg m^{-3}, and the difference between their density and that of the medium is about four times greater than it is in *Chara*. Thus the energy made available to do work by the falling of the protoplast is 5×10^{-21} J, approximately the energy needed to open an ion channel. However, since the cytoplasmic volume (6×10^{-15} m^3) of a columella cell is much smaller than that of a *Chara* internodal cell, it only takes 5.4×10^{-18} mol ($= 3.3 \times 10^6$ Ca^{2+}) to raise the concentration from 10^{-4} to 10^{-3} mol m^{-3}. A single activated channel can accomplish this in 1 s, and thus it is possible for the gravitational pressure model to explain gravity sensing in higher plant cells.

Is the gravitational pressure model better than the statolith model in explaining gravity sensing in higher plant cells? The statolith model has been weak in explaining why starchless mutants are 21–31% as efficient as the wild type in sensing low gravitational signals and do sense gravity at 1 *g* (Casper and Pickard 1989, Kiss et al. 1989, Sack 1991). According to the gravitational pressure model, the starchless mutants should sense gravity, but their sensitivity should be less than the wild type in proportion to the contribution of starch to the total mass of the protoplast. We calculate that the starch contributes 77% to the mass of the protoplast and thus the mutants should sense gravity about 23% as well as the wild type (Wayne et al. 1990). Thus the gravitational pressure model, even though it is new (Cornford 1966, C. Darwin 1889, F. Darwin 1887, Planck 1936, 1949), is more robust than the statolith model in explaining gravity sensing in the cells of characean internodes and higher plants.

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