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GRAVITY RECEPTORS AND RESPONSES

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OVERVIEW---Components of G sensing and response processes in plants. The overall process may be divided conveniently into at least four components or stages: (a) Stimulus susception: a physical event, characteristically the input to the G receptor system of environmental information about the G force magnitude, its vector direction, or both; (b) Information perception: an influence of susception on some biological structure or process that can be described as the transformation of environmental information into a biologically meaningful change; (c) Information transport: the export, if required, of an influence (often chemical) to cells and organs other than those at the sensor location; and (d) biological response: almost always (in plants) a growth change of some kind. Some analysts of the process identify, between (b) and (c), an additional stage, transduction, which would emphasize the importance of a transformation from one form of information to another, for example from mechanical statolith displacement to an electric, chemical, or other alteration that was its indirect result.

These four (or five) stages are temporally sequential. Even if we cannot confidently identify all that occurs at each stage, it seems evident that during transduction and transport we must be dealing with matters to be found relatively late in the information flow rather than at the perception stage. As we learn more and more about the roles played by plant hormones which condition the G responses, we are not necessarily able to understand better the mechanism(s) of perception which should be our focus in this Session. However, if by asking the right questions and being lucky with our experiments perhaps we can discover how some process (such as sedimentation of protoplasmic organelles) dictates what happens down stream in the information flow sequence.

GRAVITY FORCE AS A CONTINUOUS VARIABLE

Gravity is different things to different specialists. To some, nominal zero G is a stress to which hominids "adapt." Chronic G forces above zero but less than unity may seem important as experimental conditions chiefly to discover if there is a G threshold above which certain stress responses (euphemistically called adaptation) can be endured without progressive unacceptable sequelae. From that view point unit G is especially important as a "control," easily accessible on earth and supplied in orbit only by a centrifuge. However, plant and animal physiologists who work with small organisms are apt to consider gravity not necessarily as a stress but in a general sense as an environmental factor — one of the top three or four in order of importance to organisms. Like other conditions that affect plants these scientists must be able to control experimentally the G force vector direction and intensity over the full range of possible G levels from nominally zero to as far above 1 G as may seem

scientifically interesting. Thus, viewing G as a continuous experimental variable, we tend to think of the control condition not as 1 G but as weightlessness. Unit G becomes one of many abscissal G levels that occur when plotting the G function of a particular biological effect. This view point has not been readily accepted by some experts in space medicine; it is widespread in the general biological community.

GRAVITY SENSING AS A CENTRAL QUESTION FOR UNDERSTANDING HOW GRAVITY IS IMPORTANT TO PLANTS

For the better part of a century, plant physiologists have recorded a large number of descriptive studies of plant responses to gravity — more precisely to experimentally controlled changes in the direction in which the earth's gravity force acts on the plant. Relatively recent advances in methodology and improved biological and biochemical background information have encouraged the belief that we may be on the verge of dramatically improved understanding of the mechanism(s) by which gravity is sensed and those by which biological responses are generated. Nevertheless, we are still at a stage in our science where purely descriptive studies are urgently needed. Only infrequently have our theories been challenged by decisive experimental tests. Since the experimental potential for gravitational physiology has been dramatically enhanced in the last three decades by the promise of full control over the total range of experimentally applied G forces, a large number of new questions arise which call for new exploratory experiments to describe quantitatively the gravity sensing process in test organisms. Gravity sensing, although not a new area of study, has enjoyed greatly increased priority as a process to be studied by new methods created or enhanced by space flight technology. Physiologists, each in his own phylogenetic area of choice, seem to be in at least intuitive agreement that scientific progress is highly likely in the area of gravity sensing by exploiting the new technology. Broadly stated the question is: How is gravity important to plants? The central question that now drives most experimental designs is: How does the organism sense gravity?

TOOLS FOR EXPERIMENTATION

Exploration or experimentation with biological responses to any environmental factor requires control and quantitative manipulation of the factor of interest, in our case, the gravity force. It is interesting that the three major tools needed for creating, maintaining, or simulating G levels are all rotating machines.

The centrifuge probably is the most familiar. In earth laboratories centrifuges have been used to impose G forces ranging up to about 500 G for long periods in exploratory experiments with small plant seedlings (Gray and Edwards, 1955; Brown, 1983). For small organisms only a few G units above normal may be considered non-stressful and can contribute to studies of G sensing in the hypergravity G range (Brown et al, 1975). At much higher forces (10s or 100s of G units) stress reactions patently dominate even though the test species often adapts morphologically to growth in the strange environment.

For application to space experimentation various advisory groups have repeated essentially the same recommendation urging a "1 G control" aboard the spacecrafts although only recently has the recommendation been implemented, first by Soviet and later by ESA experimenters.

A unit G control in space also would be subjected to all known and unknown artifactious influences of the spacecraft (shock and vibration, for example) and of its environment (especially ionizing radiation). If all such artifacts were understood and could be measured, it would be possible to perform adequate control experiments on earth. However, skeptics always will be hard to convince that there are not some unknown influences which could deceive the investigators. The least expensive way to allay such fears would be to provide the often recommended 1 G control centrifuge in space even though the important issue really has little to do with biological effects of G forces per se. There remains, as a most compelling argument for flying on-board centrifuges, the need to access the hypogravity region of the G parameter, $0<G<1$. (Cf. contribution of D. K. Chapman in this report.)

Potentially the unit G condition also can be achieved in space by rotating the space vehicle about its center of mass. However, if we want not merely to avoid the necessity for humans' adaptation to microgravity but also want to carry out scientific experiments in hypogravity, a centrifuge would still be required, in that case with its rotational axis exactly coincident with that of the rotating space vehicle.

The centrifuge has been used on earth to extrapolate data from a series of tests at different hypergravity G levels to the ordinate axis intercept which thereby becomes a qualified estimate of what value of the measured parameter would obtain if the test could be performed at zero G. The qualification of course, is the assumption of linearity (or some other function) beyond the range accessible to experimentation. In a very few cases the assumption of linearity was disproven but at this stage of our understanding of the effects of protracted hypogravity it is impossible to generalize.

The clinostat (Sachs, 1882) is another rotating device widely used by plant physiologists to simulate hypogravity conditions on earth. It is described and evaluated by D. K. Chapman in this report. The simulated condition of zero G, achieved by clinostatting generally is referred to as "gravity compensation". How well that condition gives biological responses which are the same as those of tests in free fall remains a question that must be addressed empirically. Less than a handful of such comparisons have been accomplished and the conclusions were not in agreement (Lyon, 1968; Merkys et al, 1975; Brown et al, 1974; Brown and Chapman, 1984). It does not seem prudent to generalize at this stage of our science (Brown et al, 1976).

The rotating machine most recently added to our list of tools for experimentation is the spacecraft in earth orbit. Its radius of rotation (about 7×10^6 km) is somewhat larger than that of our earthbound centrifuges and clinostats. Its rotation rate in near earth orbit is much less (approximately 2×10^4 Hz). In stable circular orbit the G force at the center of gravity of the spacecraft closely approximates zero in the sense that no force other than gravity perturbs it; thus it establishes the ideal condition of free fall.

By itself, the spacecraft in orbit is theoretically capable of providing only one G value, nominally zero. However, by combining the satellite's potential with the capability of an onboard centrifuge, an experimenter can attain a protracted G force environment of any desired intensity, from zero to however much his experiment requires. The centrifuge is needed to impose a controlled, constant, centripetal force on the test subject otherwise in a state of free fall.

It may be of interest, for those experiments which require a very low G environmental condition, that the centrifuge axis should remain parallel to the orbital axis of rotation of the spacecraft. Whether the spacecraft is gravity gradient stabilized, or rotates slowly in its orbital plane, makes little difference: However, rapid spacecraft maneuvers can produce gyroscopic effects which should be considered. They may or may not be small enough to be ignored.

TO SENSE GRAVITY DOES ANYTHING HAVE TO MOVE?

Gravity perception can be accomplished by a variety of different mechanisms. Given that something is being influenced by gravity (or by an equivalent inertial force) that influence can be detected by dozens of physical or physical chemical mechanisms devised by engineers and physicists as well as by those, whose numbers we are in doubt, that were invented by biological systems in the course of their evolution.

For those devices invented by scientists, their mechanisms seem to have nothing in common except that all are based on ways of detecting movement. Many such devices have been invented and their detectors, amplifiers, and methods of readout are diverse. It would be arrogant for us to pretend that biological means for detecting mass movement are so much less sophisticated that only one or even only a few methods of gravity detection are employed by organisms. Nevertheless, over the past century plant physiologists have been prone to generalize (at least implicitly) the amyloplast sedimentation mechanism not only as the earliest process in G perception but as if it were, in principle, the only device plants learned to use for detecting gravity susception.

To put the matter in perspective three things should be kept in mind. (a) In spite of widespread occurrence of patently sedimenting organelles (statoliths such as large starch-filled amyloplasts or inorganic crystals, viz. barium sulfate) there are numerous examples of gravisensitive plant organs whose cells do not contain mobile organelles sufficiently more or less dense than the cytosol so that they sediment under conditions that prevail for G responding plants. According, in statocytes devoid of starch loaded amyloplasts some less obvious mechanism must exist to account for the evident consequences of gravity susception. Where no obviously functional statoliths have yet been found, we should not assume that those cells are incapable of sensing gravity. (b) It is impossible for any bioaccelerometer or for any man-made device to detect the susception of gravity unless something moves. Whether we call the perturbation falling, twisting, stretching, bending, compression, displacement, stratification, sedimentation, acceleration, or altered momentum cannot change the fact that the act of susception must be to alter something's position, shape, or acceleration. That categorical conclusion

is based on a fundamental physical principle. (c) Gravity is a body force. Acting on every particle of mass in an object, it imparts to that object its weight. An inertial force also is a body force. Acting on every particle of mass in an object, if unopposed, it gives to that object an acceleration. According to the Principle of Equivalence, it is quite impossible for experiments to differentiate between inertial forces and gravitational forces within one frame of reference. By placing an object in earth orbit it becomes weightless because it continues to be acted on only by a gravitational force. Therefore it is better to refer to its condition as free fall rather than as zero gravity. All other forces that could oppose free fall and establish equilibrium (hence weight) are absent. A particle of mass in orbit is at rest in an inertial reference frame. It remains in uniform motion as long as no other force acts on it. Because inertial and gravitation forces are equivalent, a centripetal force of any desired magnitude applied to the particle produces the same effect as would a gravitational force of the same magnitude. This is the basis for establishing a 1 G "control" condition in a satellite.

A suggested subtopic of this Session Item was, "Could gravity responses be pressure responses?" In the sense that a pressure change is suggested as an alternative to a movement, the answer is emphatically no, for reasons stated above. However, whatever moves could be responsible for (or a consequence of) a pressure change. Pumping up a flat automobile tire, for example, leads to both a small amplitude movement (centimeters) and large change of pressure (from ca. 100 k Pa to ca. 300 k Pa). It is of no consequence that we are accustomed to measuring tire inflation with a pressure gage instead of a tape measure (unless we "eyeball it" in which case the distention is estimated, not the pressure.)

With respect to plant cells, Björkman (1988) argued against a G sensor mechanism based on cells' manometric versatility, among other reasons because of the large normal fluctuations of resting pressures in plant cells. Normally cells in growing organs carry a mean pressure of about 300 to 600 k Pa above atmospheric (101.3 k Pa). However, over time during the growth process and under different conditions of water availability, extremes of internal pressures in plant cells may fall as low as -1500 k Pa and as high as +2000 k Pa, limits which are conservative estimates. Such enormous fluctuations would make it very difficult for a plant organ to detect (and to reliably interpret as gravity induced) pressure changes of very much smaller magnitude.

Moreover, by bending and restraining gravisensitive plant shoots and roots, the contralateral stretching and compression of the growing organ does not "fool" the G sensing mechanism. When released from constraint the tropistic response proceeds as would be expected from an apically located sensor that perceives only the G vector. Thus it becomes, if not impossible, at least very awkward to attempt construction of a G sensing theory that depends at any stage on a bioaccelerometer measurement of internal cell or tissue pressure.

CONCLUSION

In both animals and plants those responses which follow the act of sensing gravity ultimately involve whole organs---often the whole organism. Cell specialization is well developed in higher organisms that sense gravity. In

plants the sensor function usually resides mostly in a small group of cells, less than 1% of total tissue mass (rarely in only a single cell). These cells, the sensing organ, is sometimes referred to as a bioaccelerometer. It responds to gravity susception always by some kind of movement. In most cases this involves sedimentation of mobile organelles or stratification of zones of the cytoplasm. There is no evidence that G perception involves cooperation between cells although the consequences of G sensing undoubtedly show summation of activities of all sensor cells. Thus G perception in plants is a uniquely cellular function as it must be where it is accomplished in unicellular forms. The sensing-response process can be divided, at least conceptually, into several stages. Recent advances have told us more about how organisms, especially plants, use the gravitational information they acquire. When we are able to fully exploit the potential of experiments in microgravity and at any other gravity level the experiments require, we may find progress on how plants acquire gravitational information may outdistance that on other areas of gravitational biology.

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