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Advances in Space Research 39 (2007) 1119–1126

ADVANCES IN SPACE RESEARCH
(a COSPAR publication)

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Noise amplification of plant gravisensing

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Received 14 September 2006; received in revised form 30 November 2006; accepted 4 December 2006

Abstract

A common problem in sensory physiology is the detection of weak signals, such as that produced by the repositioning of statoliths (amyloplasts) in gravisensing cells, from a noisy background. As in other studied biological mechanosensory systems, it is conceivable that the gravisensing process may be amplified by stochastic resonance and nonlinear noise-assisted effects. We therefore investigated the possible dependency of gravisensing on vibrational or thermodynamic noise by examining the effect of external oscillation and temperature on the rate of gravitropic curvature in flax (*Linum usitatissimum* L.) roots. Roots were oscillated for 15 min prior to or during gravistimulation, either parallel or perpendicular to the root axis. The effect of oscillation was dependent on its direction as well as frequency and amplitude. Initial curvature was most effectively enhanced by vertical oscillations of 5 Hz and 0.5 mm amplitude prior to reorientation. Vertically oscillated roots reached half-maximal curvature 32 min after reorientation, about 18 min earlier than non-oscillated roots. The enhancing effect of vibration on curvature subsided with a half-time of about 20 min. The temperature dependency of the graviresponse indicated that thermodynamic noise also impacted gravity perception. For vibrations and temperature studies, the presentation times decreased almost 6-fold. Our data indicate that gravisensing may depend on or be enhanced by thermodynamic or mechanical noise.

Keywords: Gravisensing; Sensory physiology; Signal amplification; Vibration; Thermodynamic noise

1. Introduction

The orientation of plants relative to the gravity vector is essential for plant growth and development because plants organize their growth pattern to optimize root and shoot growth. Growth, especially of seedlings, is primarily determined by gravity and light and ensures the most efficient spatial configuration of roots for anchorage, water acquisition and mineral uptake from the soil, and for the capture of sunlight for photosynthesis in aboveground parts.

Gravitropism begins with gravisensing (*perception*), during which the physical information about the orientation of the gravity vector is sensed, often in specialized statocytes. These sensory cells perceive the mechanical signal and generate a biochemical signal. The signal *transduction* results in a physiological message, which is subsequently transmitted to the target region (*transmission*), where subsequent response occurs in the form of modulated tissue growth (*response*) (Björkman, 1988; Sack, 1997; Kiss, 2000). Despite more than a century of research, the exact mechanism of plant gravity sensing is still hypothetical. Although multiple mechanisms of gravity perception may exist (Sack, 1997; Hasenstein, 1999; Kiss, 2000), the perception is mediated by mass-sensitive structures most likely dense plastids (amyloplasts) or vesicles (statoliths) and is described as "starch-statolith hypothesis" (Volkmann and Sievers, 1979; Sack, 1991; Sack, 1997; Salisbury, 1993; Kiss et al., 1996; Hasenstein, 1999).

The traditional concept of gravisensing is based on the energy derived from the potential energy of the moving mass, which must be greater than the background thermal energy of the cells. These concepts are supported

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doi:10.1016/j.asr.2006.12.005

by a weaker graviresponse in mutants that cannot produce starch (Caspar and Pickard, 1989; Kiss et al., 1989). Theoretical calculations regarding the energy from the displacement of the sedimenting statoliths are based on assumptions on the size, and density of statoliths and viscosity of the cytoplasm, which cannot be conclusively determined (Kiss, 2000; Kondrachuk, 2001). If the signal energy is at threshold level (Johnsson and Pickard, 1979), it seems probable that (plant) cells possess mechanisms to detect and/or amplify the weak stimulus signal from a noisy background within the cell to initiate subsequent steps in the perception, transduction and response sequence. The sensitivity of plants to about 10^{-4} g (Shen-Miller et al., 1968), suggests that some gravity-sensing systems function at threshold levels lower than the normal 1*g* environment present during their evolution (Brown et al., 1995), and explains why starch-deficient/starchless mutants are able to respond to gravity (Kiss et al., 1996). Extensive evidence supports the plastid-based gravitropic sensing in plants (Volkmann and Sievers, 1979; Sack, 1991 and Sack, 1997; Salisbury, 1993; Kiss et al., 1996; Blancaflor et al., 1998; Hasenstein, 1999; Ma and Hasenstein, 2006), but the initial step of gravity sensing remains elusive. It is possible that the evolution of starch-filled plastids as gravity susceptors was paralleled by cellular structure that served as receptor(s).

The findings that starchless and starch-deficient mutants are capable of gravisensing (Caspar and Pickard, 1989; Kiss et al., 1996), and that plants exhibit gravitropism in response to fractional *g* levels (Brown et al., 1995) suggest that the gravity sensing system operates well below the 1-g force typically acting upon the sensor. The high sensitivity combined with a substantial cellular movements and saltatory motions (Sack et al., 1984; Saito et al., 2005) indicates that plant statocytes operate in the presence of substantial mechanical background noise.

Noise is present in all physical, chemical, and biological systems and is a function of life itself. Despite its general tendency to obscure signals, it may also play a constructive role in the processing and transfer of information. Stochastic resonance (Kaiser, 2000) is based on random processes and is described as the dynamic motion of a particle or system state point in a bistable potential (Gammaitoni et al., 1989a; Gammaitoni et al., 1989b; Jung and Hanggi, 1991; Moss, 2000), the response of which to a weak stimulus may be optimized by the presence of an optimal level of noise. The non-dynamic, statistical view of stochastic resonance states that, in principle, for stochastic resonance to function in a system, it only needs three elements: a threshold, a sub-threshold signal that carries some information, and internal or external noise (Gingl et al., 1995; Moss, 2000). When noise is added to the sub-threshold signal, threshold-crossings occur in the form of pulses, which carry a significant amount of information about the sub-threshold signal. It has been mathematically demonstrated that threshold-crossing rate can be exponentially sensitive to the weak signal, thereby amplifying it (Moss, 2000).

Previous research (Douglass et al., 1993; Wiesenfeld and Moss, 1995) has shown that the detection of weak signals in mechano-receptors may be promoted by noise. Considering the nonlinear characteristics of the temporal dynamics exhibited in plant root gravitropic response, we explored the dependency of the graviresponse on added mechanical noise. The substantial amplification of the weak gravistimulus by noise indicates that the dynamic motion in statocytes (Sack et al., 1984; Saito et al., 2005) affects gravisensing. We test the hypothesis that "threshold crossings" occur more frequently as a response to added mechanical perturbation (noise) via stochastic resonance similar to the experimental design of Douglass et al. (1993) who used temperature and single-frequency vibrations. We examine the influence of noise on gravity sensing and present evidence that the dynamic motion of the primary sensors not only contributes to gravisensing but may well be a general principle of plant mechanosensing.

2. Materials and methods

2.1. Plant material

Flax (*Linum usitatissimum* L.) seeds were soaked in distilled water for 10 min, then placed on strips of germination paper layered onto the surface of 20 mL, 2% (w/v) agar in plastic square Petri dishes (90 mm × 90 mm). The Petri dishes were wrapped with Parafilm and maintained vertical for root emergence along the surface of the agar. Seeds were germinated at 23 °C in the dark for 24 h, and seedlings were used when roots reached an average length of 5 mm. All subsequent experiments were conducted under dim fluorescent light (< 0.5 µmol s^{-1} m^{-2}).

2.2. Mechanical oscillation

The experimental chamber was mounted on a voice coil shaker (Fig. 1, V101/2 with dedicated PA 25E amplifier; LDS systems, Middleton, WI, USA), which was driven through a computer-controlled frequency generator that produced variable waveforms. The waveform signal was subsequently amplified (Fig. 1). The Petri dish with seedlings was oscillated for 15 min prior to the onset of gravistimulation, at frequencies of 5, 10, or 20 Hz, and amplitudes of 0.5 mm. The direction of the oscillation was parallel to the root axis. The effect of oscillations on graviresponse and gravisensitivity was examined. Accelerometer-based measurements of the resulting waveform showed that although a defined signal was provided, the Petri dish and seeds received a noisy (not defined by a single frequency) stimulation, presumably resulting from superposition of electronic and mechanical influences. Therefore, we refer to noise and not frequency amplification.