

Guidance of circumnutation of climbing bean stems: An ecological exploration

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Abstract In this report we explore the guidance of circumnutation of climbing bean stems under the light of general rho/tau theory, a theory that aims to explain how living organisms guide goal-directed movements ecologically. We present some preliminary results on the control of circumnutation by climbing beans, and explore the possibility that the power of movement in plants, more generally, is controlled under ecological principles.

Keywords: Plant shoot circumnutation; Tau theory; ecological psychology.

Introduction

Living organisms guide the movement of effector organs or cells in response to stimuli to make, or avoid, contact with things—be it a bee flitting from flower to flower, a gibbon swinging from branch to branch, or a peregrine falcon diving on a flying pigeon. Strikingly enough, plants, unlike animals, are commonly believed to remain still, with their behavioural repertoire reducing, or so the story goes, to invariant tropistic—Jacques Loeb’s (1918) ‘forced reactions’—or nastic responses implemented in the form of sets of fixed reflexes. The need to control their movements is thereby eliminated or seriously undermined. And yet plants are as much in the move as any other living organism. Plant stems grow alternatively on different sides, which results in the stem bending in one direction, then in the opposite one. But there is virtually no growing part of any single plant that fails to exhibit a movement of nutation (Mugnai et al., 2007). Not only the tips of shoots sway in circles as they grow, but also leaves and roots exhibit ‘revolving nutation’, as Julius von Sachs called it, or *circumnutation*, to use the expression coined by Charles Darwin. Circumnutation, we may say, is universal. All plants do it. Shoots of climbing plants guide their movements to reach a support; roots navigate belowground, guiding their movements to secure nutrients intake; young and terminal leaves display helical and rotational oscillatory movements, etc. (Darwin, 1975; Darwin and Darwin, 1880).

In this report, we consider the possibility that *the power of movement in plants*, to echo Darwin and his son’s seminal work, is not forced, or hardwired, but rather appropriately controlled as much as the movements performed by bees, gibbons or peregrine falcons are. More specifically, we shall focus our attention on what is

53 probably the simplest form in which general circumnutation can be modified: the
54 one exhibited by twining plants, in particular, by common beans (*Phaseolus*
55 *vulgaris*) as they approach and twine spirally round supports for photosynthetic
56 purposes. Unlike leaf-climbers, tendril-bearers, and hook and root climbers that use
57 a whole new bag of tricks insofar as attachment mechanisms and stem structure and
58 function are concerned (Isnard & Silk, 2009), bean shoots rely exclusively on an
59 increase in the amplitude of an otherwise ordinary movement of circumnutation.
60 Such basic, and yet modified, revolving nutation shall be the focus of our attention.
61 In particular, we aim to explore the guidance of circumnutation of climbing bean
62 stems under, broadly speaking, Gibsonian ecological principles (Gibson, 1966;
63 1979); and more specifically, under the light of General Tau Theory (Lee 1998; Lee
64 et al., 2009).
65

66 **The control of movement in climbing plants**

67 The underlying idea that motivates the research herewith reported is the suspicion
68 that the control of movement in plants is not unlike the control of movement in
69 animals. Plants and animals, we contend, have functionally similar internal systems
70 for organizing sets of behaviours. In essence, a plant that orients towards, say, a
71 source of energy behaves in functionally the same way as an animal that runs
72 towards its prey. It is in this sense that the type of control required to perform such
73 actions is our object of study.
74

75 Nutation is due to differential cell growth, and not to changes in the state of turgidity
76 (rigidity) of cells, as is the case, for instance, in heliotropic and nyctinastic (sleep)
77 movements. Whereas the latter exploit changes in turgor pressure and are thus
78 reversible by the alternative gain and loss of cell water, the former, being dependent
79 upon growth, is irreversible. In addition, growth-related circumnutation of the stem
80 is not triggered by external forces themselves, such as temperature, gravity, or
81 day/night cycles, but is rather brought about, maintained and modified by
82 endogenous means. Plants explore, and exploration uses up energy and therefore
83 needs to be done efficiently, especially considering that growth-related movements
84 are irreversible. Control thus appears to be needed for the regular pattern of bending
85 observed to obtain. In particular, both the direction and the amplitude of nutational
86 movements require control, if the metabolic cost of irreversible but idle movements
87 is to be minimized.
88

89 With that being said, that plants or animals *control* their movements does not imply
90 that their behaviour is to be accounted for in computational or information-
91 processing terms. In fact, our working hypothesis is that both plants and animals
92 guide their movements *ecologically*—non-computationally. According to ecological
93 psychology, plants, like animals, perceive what is available in terms of biologically
94 relevant interactions (Carello et al., 2014). Plants perceive opportunities for
95 behavioural interaction with their local environment in the form of what Gibson
96 dubbed “affordances”. Climbing plants are in this way ecological *perceivers*. Vines
97 perceive possibilities for action, such as when a support is perceived as affording
98 climbing. Or take *Monstera gigantea*, a climbing vine whose seeds are able to
99 perceive an affordance (climb-ability) skototopically, as they grow towards
100 darkness (Turvey et al., 1981).
101

102 Under this framework, the proper unit of analysis is the whole organism-
103 environment system as such (Richardson et al., 2008). A climbing plant and its

104 support constitute an ecologically coupled system in which the action of twining and
105 the perception of affordances form a continuous and cyclic loop. Despite things
106 being in constant flux, some relations remain unchanged, and organisms can pick
107 them up. This information is relational, and takes the form of invariant properties of
108 the underlying structure of an ever-changing environment that can in principle be
109 directly detected. Ecological psychologists say that environmental information is
110 *specificational*: information in the vicinity of a climber specifies ways for the plant
111 to interact with features, such as the support standing nearby. Our working
112 hypothesis is that plants, like animals, pick up the invariant structure of an ever-
113 changing environment. General rho/tau theory puts some flesh onto this framework
114 for empirical test.
115

116 **General Rho/Tau Theory**

117 *General rho/tau theory* (Lee 1998; Lee et al. 2009) aims to explain how living
118 organisms guide goal-directed movements endogenously by using prescriptive and
119 perceptual information. Up to 2009, the theory dealt with guidance of movement in
120 animals (see Lee et al., 2009). In this section we review its main tenets, and
121 elaborate on how the theory applies to plants too. In a nutshell, the main points of
122 general rho/tau theory are as follows:
123

124 (i) Purposeful, goal-directed, movement entails guiding the trajectory of an effector
125 to a goal across a motion-gap; that is, it requires the guidance of the closure of
126 motion-gaps, where a motion-gap is defined as the changing gap between a current
127 state and a goal state. Motion-gaps may occur across a variety of dimensions—e.g.,
128 distance when reaching, angle when shifting gaze or direction of movement,
129 pressure when gripping, pitch and loudness when vocalizing or making a noise,
130 intraoral pressure when suckling, etc.
131

132 (ii) Closing a motion-gap requires:
133

134 (a) generating prescribing information to specify the intended trajectory of the gap;
135 (b) picking up perceptual information from the stimulus about how the trajectory is
136 actually evolving;
137

138 and
139

140 (c) regulating the motor information to make the prescribing and perceptual
141 information match.
142

143 (iii) The primary perceptual information used in guiding a goal-directed movement
144 is transmitted through the medium of *power* (rate of flow of energy), and takes the
145 form of the *rho/tau of a power gap* (the tau of a gap of magnitude, X , is the time it
146 will take the gap to close at the current closure rate). The tau of the gap equals the
147 current magnitude, X , of the gap divided by the current rate of change of X , viz. \dot{X} .
148 The defining equation is:
149

$$150 \tau(X) = X / \dot{X}$$

151

152 The unit of *tau* is time. Since rho and tau are mathematical duals—rho of a gap =
153 1/tau of the gap—, for ease of exposition, rho rather than tau of a gap is used here.
154 We shall then say that the information used for guiding the closing (or opening) of a
155 motion-gap is the rho of the gap, the proportionate rate of closing (or opening) of the
156 gap. Rho of gap X at any time t equals the current rate of change of the size of the
157 gap divided by the current size of the gap. Thus,

$$158 \quad (1) \quad \rho(X,t) = \dot{X} / X$$

159 where the dot indicates the time derivative. Rho of a motion-gap is, in principle,
160 directly perceptible by all known perceptual systems: in contrast, the size of a
161 motion-gap, or any of its time derivatives (velocity, acceleration etc), is not directly
162 perceptible or specified in the stimulus (Lee, 1998), requiring a scaling factor.

163
164
165 (iv) Synchronizing the closing of two gaps, as when catching a ball, is achieved by
166 rho-coupling the gaps, by keeping the rho of one gap (e.g., hand to catching place) in
167 constant proportion with the rho of another gap (e.g., ball to catching place). Hence,
168 the general rho-coupling equation

$$169 \quad (2) \quad \rho(Y,t) = \lambda_{Y,X} \rho(X,t)$$

170
171 where Y and X are the gaps, t is time and $\lambda_{Y,X}$ is the coupling factor, which
172 determines the shape of the velocity profile of Y relative to X.

173
174
175 (v) By rho-coupling the motion-gap (via perceptual information) onto a changing
176 ‘guiding-gap’ generated endogenously, prescribes how a motion-gap, Y, should
177 close. Analyses of many skilled movements indicate a guiding-gap, G, that changes
178 at a constant accelerating rate from rest. Thus, an extrinsic motion-gap, Y, is guided
179 by making the movement follow the equation

$$180 \quad (3) \quad \rho(Y,t) = \lambda_{Y,G} \rho(G,t,T_G)$$

181
182 where T_G is the time the guiding gap G takes to close (or open). Here

$$183 \quad (4) \quad \rho(G,t,T_G) = 2t / (t^2 - T_G^2)$$

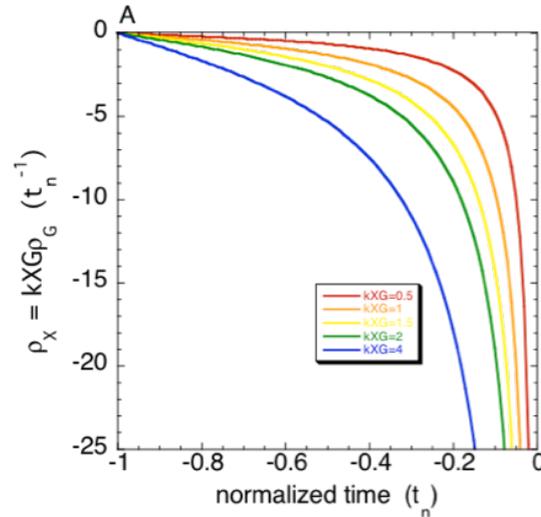
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185 as derived from Newton’s equations of motion, where time t runs from 0 to T_G .¹

186
187
188
189 Figures 1A-1D below depict the effect of the coupling factor, $\lambda_{X,G}$, on rhoG-
190 guidance of gap X following the equation $\rho(X,t) = \lambda_{X,G} \rho(X,t,T_G)$.²

191

¹ The degree of rhoG-guidance of Y is assessed by linearly regressing the measured value, $\rho(Y,t)$, on the mathematical function $\rho(G,t,T_G)$ (Schogler et al. 2008). The criterion used as evidence of rhoG-guidance is that more than 95% of the variance in the data is accounted for by Eq. (3) (i.e., $r^2 > 0.95$). When this criterion is not met for a whole movement, the maximum percentage of the data extending to the end of the movement that satisfies the criterion is computed. The regression slope measures $\lambda_{Y,G}$.

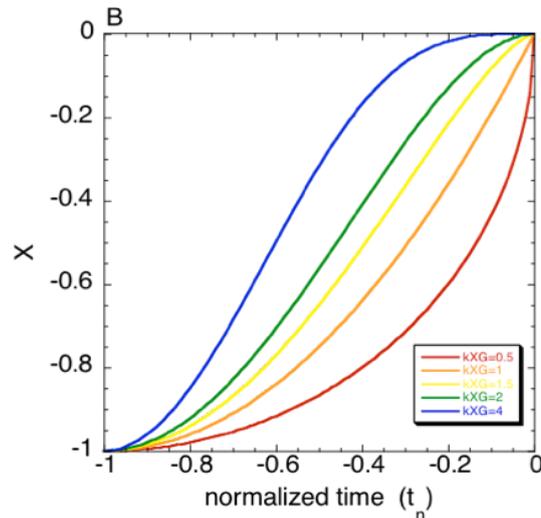
² The values of X, t, and TG have been normalized for clarity, without loss of generality in all figures: the normalized size of the gap X equals 1; the gap starts to close at normalized time -1 and ends closure at normalized time 0; the normalized duration of closure, TG, equals 1.



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Figure 1A. Effect of the coupling factor, $\lambda_{X,G}$, on rhoG-guidance of gap X following the equation

$$\rho(X,t) = \lambda_{X,G}(X,t,T_G). \text{ (A) } \rho_X, \text{ the rho of gap.}$$



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Figure 1B. Effect of the coupling factor, $\lambda_{X,G}$, on rhoG-guidance of gap X following the equation

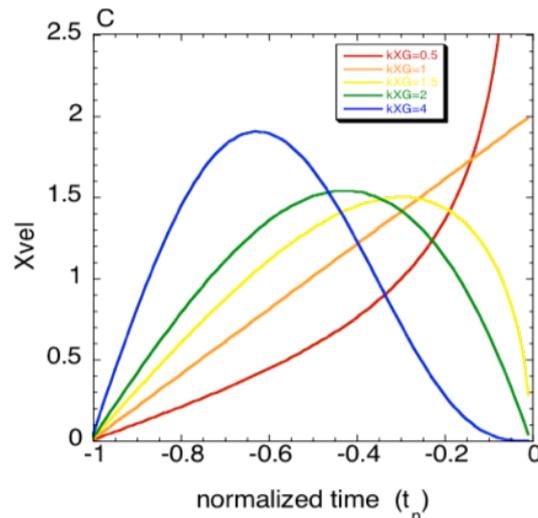
$$\rho(X,t) = \lambda_{X,G}(X,t,T_G). \text{ (B) } X, \text{ the size of the gap.}$$

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A motion-gap that follows Eqs. (3) and (4) is said to be rhoG-guided. The kinematic form of the prescribed motion-gap is defined by Eqs. (3) & (4). There are two adjustable parameters,

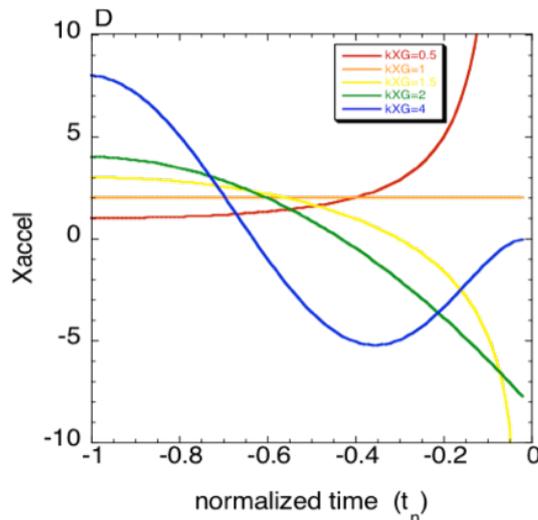
$$\lambda_{\gamma,G} \text{ and, } T_G$$

which specify, respectively, the shape of the velocity profile and the duration of the motion-gap. The velocity profile is single-peaked and the position of the peak is determined by the value of $\lambda_{\gamma,G}$ (Fig. 1C).



210
211 Figure 1C. Effect of the coupling factor, $\lambda_{x,G}$, on rhoG-guidance of gap X following the equation
212 $\rho(X,t) = \lambda_{x,G}(X,t,T_G)$. (C) Xvel, the velocity of closure of the gap.

213
214 When $\lambda_{y,G} > 1$ the gap-closing movement first accelerates at a varying rate up to a
215 peak velocity and then immediately decelerates at a varying rate to the goal (Fig.
216 1D).



218
219 Figure 1D. Effect of the coupling factor, $\lambda_{x,G}$, on rhoG-guidance of gap X following the equation
220 $\rho(X,t) = \lambda_{x,G}(X,t,T_G)$. (D) Xaccel, the acceleration of closure of the gap.

221
222 Gently touching an object, so that the velocity of approach is zero when the object is
223 reached, requires $\lambda_{y,G} \geq 2$. Hitting something, so that when the object is reached the
224 velocity of approach is positive, requires $\lambda_{y,G} < 2$. Thus, rhoG-guidance of motion-
225 gaps is a simple way of regulating goal-directed movement.

226
227 General rho/tau theory has been tested successfully across a number of species and
228 activities (Lee et al. 2009). High-resolution movement analysis has yielded evidence
229 for rho/tauG-guidance of motion-gaps that span a range of skills, including newborn
230 babies suckling (Craig & Lee 1999), infants catching (van der Meer et al. 1994),
231 adults reaching (Lee et al. 1999), controlling gaze (Grealy et al. 1999; Lee 2005),
232 intercepting (Lee et al. 2001), putting at golf (Craig et al., 2000), flying aircraft
233 (Padfield 2011), singing and playing music (Schogler et al. 2008), and flies landing

234 (Wagner 1982), hummingbirds feeding (Delafield-Butt et al. 2010). Also, evidence
235 of rho has been found in the electrical activity in the brains of locusts (Rind &
236 Simmons 1999), pigeons (Sun and Frost 1998), monkeys (Merchant et al. 2004) and
237 humans (van der Weel et al. 2009), and in a unicellular paramecium (Delafield-Butt
238 et. al 2012).

239
240 There are two basic types of movement: *propriospecific* movements that are specific
241 to the individual's body and *expropriospecific* movements that are specific to the
242 organism's relation to the environment and other organisms. In animals, there are
243 vital propriospecific movements within the skeletal, muscular, respiratory, cardio-
244 vascular, lymph-vascular, endocrine, digestive, excretory, and reproductive systems.
245 Similar life-sustaining propriospecific movements occur in plants, cells, and fungi.
246 Vital expropriospecific movements in animals include moving in the environment,
247 grasping objects, feeding, avoiding predators, and mating. Again, similar
248 expropriospecific movements occur in plants, cells and fungi.

249
250 In all cases, propriospecific and expropriospecific movements must be coordinated
251 to achieve functional movement. This is the essential task of the electrochemical
252 nervous and endocrine informational systems in animals. These pick up, generate
253 and integrate information for guiding movements. *Sensory* information about
254 movement is picked up by active perceptual systems, both within the body and at its
255 surface. *Prescriptive* information specifying purposive movement is generated
256 within the electrochemical informational systems. Both types of information flow
257 along channels in the body as *electrochemical power* (rate of flow of energy). The
258 information is a mathematical rho/tau function of the electrochemical power. The
259 prescriptive and sensory information are integrated in the nervous and endocrine
260 systems, resulting in rho/tau *motor* information being transmitted to contractile cells
261 in muscles in animals and, we believe, in roots and stems in plants. In animals, the
262 basic function of the nervous and endocrine systems is to organize the prescriptive,
263 sensory and motor information to achieve purposeful movement. Our working
264 hypothesis is that the same applies in plants.

265
266 Like animals, plants need ways of transmitting the prescriptive, perceptual and
267 muscular-like information around their bodies. Plants thus fall under the scope of
268 general rho/tau Theory. A bean shoot, as it grows and seeks a support with its tip,
269 circumnutates the whole shoot in its endeavour. Plants also need *perceptual* organs
270 to seek out information for guiding their effectors. They also need to generate
271 *prescribing* information to specify the movement trajectory necessary to fulfil their
272 purpose.
273

274 **Behavioural study**

275 The basic experimental paradigm in our study consisted in the analysis of plant
276 circumnutation behaviour through controlled time-lapse observation of the
277 approaching manoeuvre of a bean plant engaged in closing the gap in between its
278 shoot apex and the support that stands in its vicinity.
279

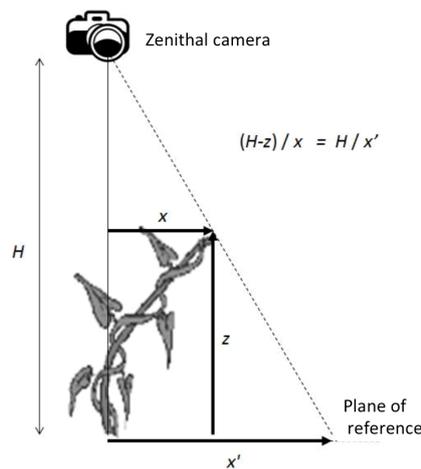
280 **Method**

281 **Subjects**

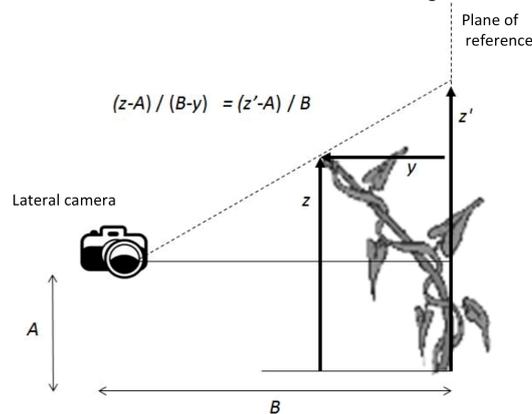
282 The experiment was conducted on bean plants (*Phaseolus vulgaris*, *Leguminosae*).
283 Healthy-looking bean seeds were selected from *Semillas Ramiro Arnedo* (Av.
284 Infante D. Juan Manuel, ed. Cinco Estrellas, 30011, Murcia, Spain). Seeds were
285 potted and kept at ambient temperature. Water levels were checked periodically to
286 maintain a hydric bedding throughout the experiment.

287 **Apparatus**

288 A potted bean plant was placed at the centre of the experimental growing chamber.
289 A single vertical pole (not shown in figures 1 and 2), placed at a distance of 50
290 centimetres from the plant centre was used as potential support for the bean to twine
291 around. Two digital single-lens webcams, one (fig. 1) at a height of 200 cms.
292 pointing vertically down with the X-axis of the picture frame closely parallel to the
293 line joining the centre of the plant (C) and the bottom of the pole; the other camera
294 (fig. 2) located at 50 cms. from the plant, pointing horizontally with the X-axis of its
295 picture frame approximately horizontal.
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299
300 Figure 1. Zenithal camera. An illustration of the experimental apparatus.



301
302
303 Figure 2. Lateral camera. An illustration of the experimental apparatus.

304 **Procedure**

305 The setting was recorded from the two view-points illustrated in figures 1 and 2.
306 Lenses were zoomed to optimize the resolution of the movement of the shoot apex.

307 From the camera recordings, the (x,y,z) coordinates of the plant's growing tip, T; the
308 bottom of the pole, P; and the centre of the plant, C, were computed—where the z-
309 axis was vertical, the (x,y) plane horizontal and the x-axis approximately parallel
310 with the line between P and C. Time-lapse records were made, the time interval
311 between frames being 30 seconds. The pole was vertical and in place during the
312 whole recording session.

313
314 We analysed the movement of the shoot-tip by digitizing the time-lapse frames. To
315 do this, we first recorded the coordinates of the shoot base, the shoot tip, and the
316 pole by digitizing those three points on one single picture frame. Subsequently, we
317 traced the movement of the shoot apex by digitizing the coordinates of the shoot tip
318 in each of the 1,034 time-lapse frames that had been recorded (both zenithal and
319 lateral), as the plant moved throughout the experiment. This series of digitized
320 points gave us a file with the 2-D coordinates of the shoot apex for each zenithal and
321 lateral picture being taken. Out of these zenithal and lateral coordinates, we obtained
322 a file with the (x', y', z') coordinates of the whole 3-D setting.

323 Because optical aberrations had to be dealt with before any further analysis could be
324 made on coordinates (x', y', z'), perspective error was measured.³ Distorted
325 coordinates (x', y', z') were transformed into coordinates (x, y, z), by:

326

327 i. Digitizing distorted coordinates (x', y', z') for both cameras (see above).

328

329 ii. Measuring distances H, A and B (figures 1 and 2, above, respectively)—A = 7 cm
330 y B = 50 cm, y H=125 cm.

331

332

333 iii. Calculating real, undistorted coordinate z out of y' following equation:

334

335
$$(1) \quad z = \frac{BH - (H - A)y'}{BH - (z' - A)y'} \cdot (z' - A) + A$$

336

337 iv. Calculating real, undistorted coordinates x and y, out of z, following equations:

338

$$\begin{cases} x = \frac{H - z}{H} \cdot x' \\ y = \frac{H - z}{H} \cdot y' \end{cases}$$

339

340

341 The (x,y) coordinates for the shoot tip were subsequently transformed into (r,A)
342 coordinates (the zenithal camera allowed us to track the (r, A) coordinates of the
343 shoot tip, where r is the horizontal radial distance of the tip from the pole, and A is
344 the angle of this radius vector from a horizontal reference direction fixed in this
345 environment). We then performed a rhoG/tauG analysis on these (r,A) coordinates.

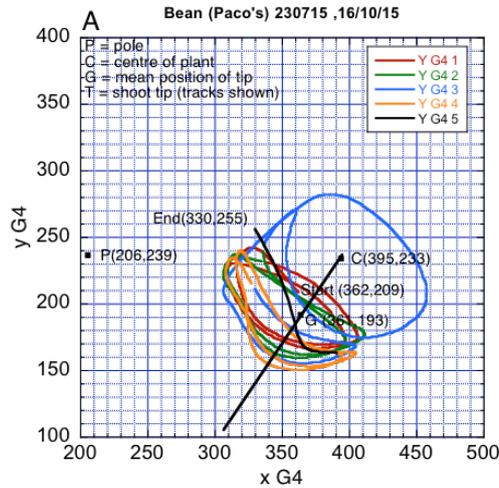
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347 **Results**

348 The following analysis is of circumnutation in the presence of the pole. In figure A,
349 shoot tip, T, appears to circumnutate around an approximately elliptical orbit,

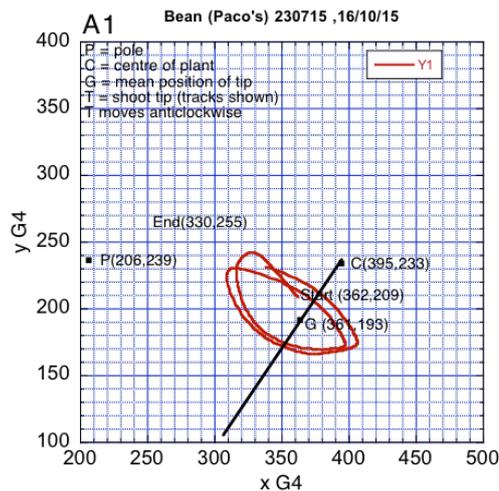
³ Optical distortion due to the webcam lens curvature was negligible and only parallax, perspective-induced error was corrected during post-processing

350 centred on the mean (x,y) position, G, of the tip. The major axis of the orbit points
 351 roughly in the general direction of the pole, P. There does not appear any systematic
 352 change over time with the orbit, except for the blue orbit.

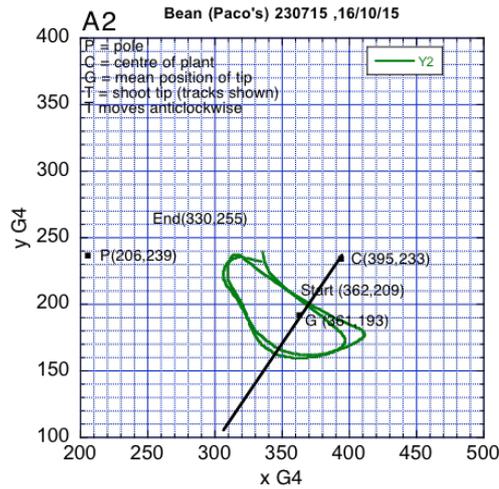


353 Figure A. Fig. A. The (x,y) tracks of the tip of the shoot. The (x,y) coordinates were smoothed with a
 354 Gaussian filter sigma 4. This was the only smoothing done in the whole analysis. The colour coding
 355 (1 red, 2 green, 3 blue, 4 orange, 5 black) refers to four successive 0.5 video minute epochs from the
 356 start of the recording, ending with a 0.1 video minute epoch. (1 video minute = 25x60 = 1500 frames.
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 358

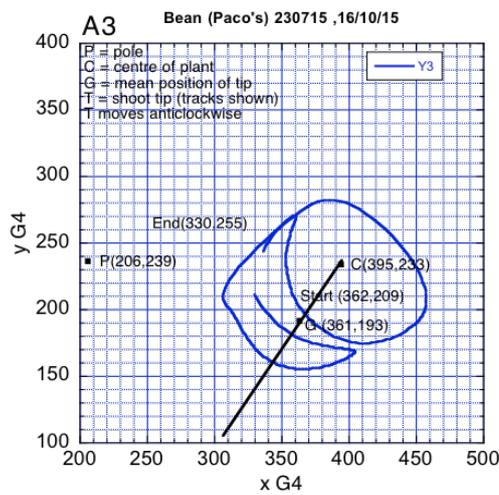
359 Figures A1-A4 below represent figure A split up into four successive 62.5 min
 360 epochs, to see whether there was any progressive shift in the orientation of the
 361 trajectory of T, or any progressive shift in the position of the trajectory along the CG
 362 line. There does not appear to be any such progressive shift in the orientation of the
 363 trajectory of T, but there appears to be some shift away from C (except for A3,
 364 which is an odd-ball).
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 366



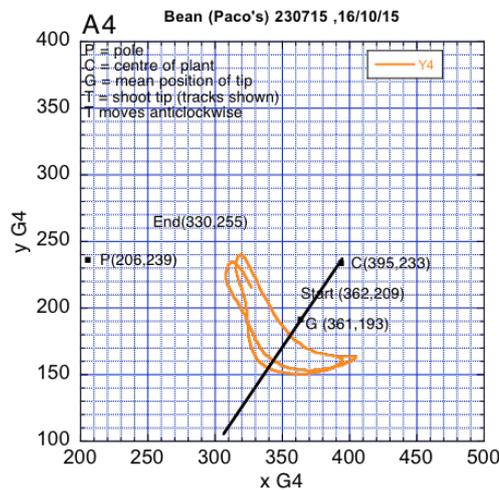
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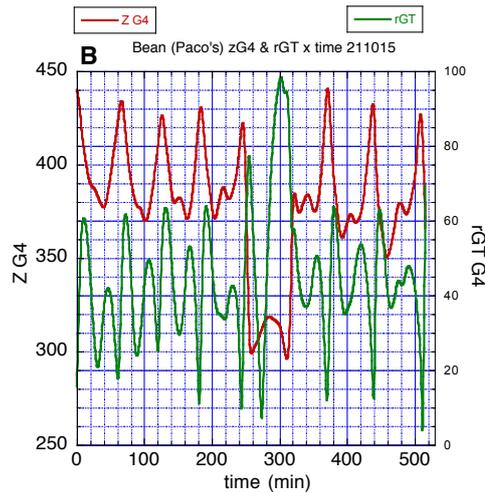
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371

372 Figure B plots, in green, against time, the radial distance from G to T (rGT) The
 373 mean strength (% of data fitting the theory with $r^2 > 0.95$) of tauG-guidance of rGT
 374 was high when rGT was decreasing, but significantly ($p < 0.01$, t-test) lower when
 375 rGT was increasing ($96.03\% \pm 0.56\%se$ vs $85.43\% \pm 3.65\%se$). At the same time,
 376 the mean k value of tauG-guidance was significantly ($p < 0.01$, t-test) *higher* when
 377 rGT was decreasing ($0.55 \pm 0.09se$ vs $0.29 \pm 0.03se$). These results indicate that the
 378 movement of the tip relative to its mean position (G) was very gently, but weakly

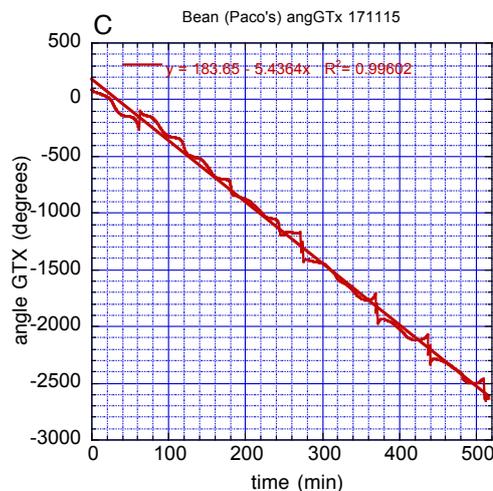
379 tauG-guided when the tip was cast out (like a fly-fishing line) but was less gently,
380 and strongly tauG-guided when it was being reeled in.

381
382 Figure B also plots, in red, the vertical z coordinate of the shoot tip. Generally
383 speaking, the tip tended to move down while it was being cast out, and move up
384 while it was being reeled in (again like a fly-fishing line). Both up and down
385 movements were strongly tauG-guided (up $95.48\% \pm 1.04\%se$; down $94.54\% \pm$
386 $0.49\%se$). The mean k values of 0.425 (up) and 0.356 (down) indicate gentle
387 approach to both the zenith and bottom.
388



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390
391 Fig. B. Plots against time of the radial distance from G to T, rGT (green) and the z
392 coordinate of T (red).
393

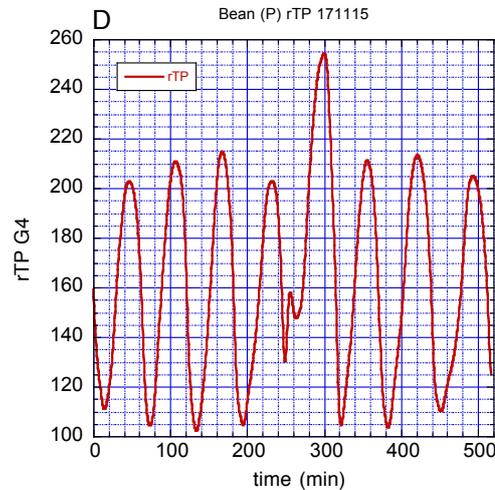
394 To obtain a measure of the angular speed of circumnutation, Figure C plots the
395 angle, GTx, between GT and the x-axis. The angle increases continuously from 0 to
396 2670 degrees, at an approximately steady speed of 10.9 degrees per minute ($r^2 =$
397 0.996), except for a sequence of small glitches.
398



399
400 Figure C. Plot of the angle GTx between GT and the x-axis.
401

402 Finally, Figure D plots the distance rTP between T and P. T was moderately
403 strongly tauG-guided when receding from and approaching P (receding 92%;

404 approaching 94%). However, it never reached the pole (see discussion section,
405 below).
406



407
408 Figure D. Plot of the distance rTP between T and P.
409

410 Discussion

411 The results reported here are congruent with the working hypothesis that climbing
412 plants resonate to specificational information of the type provided by high-level,
413 relational invariants such as rho/tau—variables that guide interactions with the
414 environment at an ecological scale. This provides grounds to argue plants perceive
415 and circumnate in their surroundings ecologically: they explore their environment
416 by picking up invariant information in the form of relational properties that can be
417 detected directly, unaided by any additional processing of information.

418
419 Nevertheless, even acknowledging the possibility that climbing plants may guide
420 their movement of circumnutation ecologically, someone may resist the parallelism
421 between plants and animals, wondering for example what sensory modality is
422 involved in the direct process of perception, or what type of non-neural substrate
423 could permit the detection of ecological information. After all, basic and cognitive
424 neuroscience appears to have a pretty good story to tell both at the level of the
425 sensory modalities involved in animal perception, as well as at the level of the neural
426 correlates involved. But, how do neuron-less living organisms cope with their
427 demands, such as perceiving an object as a potential support, despite lacking eyes or
428 ears, and a nervous system at all?

429
430 To make a long story short, general rho/tau theory is neither (sensory) modality-
431 specific nor substrate-specific (Calvo et al., 2014). Rho/tau related informational
432 variables remain specificational regardless of the sensory modality involved.
433 Consider for illustration a free-swimming cell (Delafield-Butt et al., 2013), where
434 the tau of the cell is the time needed to swim to a cathode by sensing electric fields
435 at its current rate-of-closing. Or take steering bats whose guidance is based on
436 echolocation (Lee et al., 1995). It is thus not a unique sensory modality, such as
437 vision, that drives the wheel, but rather the changes in the sensory gaps of *any*
438 *sensory modality* whatsoever. They inform us as to which opportunities for
439 behavioural output are available. As we saw earlier, one advantage of our ecological
440 understanding of perception and action is that, unlike the size of motion-gaps, or any
441 of its time derivatives (velocity, acceleration etc), rho of a motion-gap is, in

442 principle, directly perceptible by all known perceptual systems. Given that plants
443 have at their disposal a panoply of sensory modalities other than vision or hearing
444 (Chamovitz, 2012) —in fact, plants can sense up to 22 different biotic and abiotic
445 vectors (Trewavas, 2008), including electrical, magnetic, chemical, and vibrational
446 fields—, plant perception and movement can be the subject to an ecological analysis
447 in the very same way that a free-swimming cell and a bat are. Plant apices contain
448 electrical, chemical, vibrational, gravitational and optical sensory transducers that
449 afford information about the movement of the apex in relation to the environment.
450 Nevertheless, more work is needed, and the preliminary results of this report do not
451 allow us to single out one particular sensory modality to be involved in the control
452 of circumnutation.

453
454 On the other hand, general rho/tau theory is substrate-neutral. The fact that guidance
455 is partly performed intrinsically, does not mean that it should be neurally based.
456 Regardless of the type of substrate involved, what counts is whether the
457 spatiotemporal scale of processes remains ecological or not. If specificational
458 information happens to be found, for instance, at the scale of hormonal processes,
459 the relevant substrate may then be hormonal.

460
461 With that being said, plants and animals share many ‘neural’ features (Calvo,
462 submitted). A number of plant neurotransmitters have been identified (Baluška &
463 Mancuso, 2009a). The role of G-aminobutyric acid (GABA) in plant signalling, for
464 instance, is generating increasing interest (Bouché and Fromm, 2004). In fact,
465 neuroid conduction (Mackie, 1970) is a basic and widespread form of signalling. It
466 is well-known how electrical events propagate in the non-nervous cells of protists
467 and plants. Plant and animal cells conduct signals from receptor to effector sites.
468 Information is conveyed through an electro-chemical communication system
469 (Keijzer et al., 2013), and action potentials propagate multidirectionally along the
470 phloem (Baluška & Mancuso, 2009b), allowing plants to elaborate coordinated
471 responses.

472
473 In multicellular animals, relevant information takes the form of temporal changes in
474 ‘neural power’ (the rate of flow of electrochemical energy that flows along nerves,
475 either continuously as a graded potential or as trains of action potentials).
476 Prescriptive neural-power gaps are generated in the central nervous system. The
477 analysis of skilled movement in animals has permitted identification of two types of
478 prescriptive neural-power gaps: G-type and D-type, depending on whether the gap
479 closes at constant acceleration or deceleration.

480
481 In cells, micro-organisms such as bacteria, and plants, this information-bearing
482 ‘neural power’ consists in streams of ions flowing along ion channels, and thus
483 renders itself subject to the same type of analysis. Unfortunately, because our
484 recording started when the bean plant was already circumnutating, and ended when
485 it died of heat exhaustion, before it had attempted to reach the support, we are
486 unable to analysis whether the skilled movement of circumnutation performed by
487 climbing plants conforms to prescriptive neural-power gaps of G-type or D-type in
488 the control of the approach movement towards the support.

489
490 Climbing plants perform an ordinary movement of circumnutation in the early stages
491 of development. As they grow the pattern of nutation changes, and here is where we
492 suspect that such analysis would bear fruit. The sophistication of modified

493 circumnutation is something that Darwin himself had already noticed. In a
494 description of the circumnutation of *Ceropegia*, he observed:

495
496 When a tall stick was placed so as to arrest the lower and rigid
497 internodes of the *Ceropegia*, at the distance at first of 15 and then of
498 21 inches from the centre of revolution, the straight shoot slowly and
499 gradually slid up the stick, so as to become more and more highly
500 inclined, but did not pass over the summit. Then, after an interval
501 sufficient to have allowed of a semi-revolution, the shoot suddenly
502 bounded from the stick and fell over to the opposite side or point of
503 the compass, and reassumed its previous slight inclination. It now
504 recommenced revolving in its usual course, so that after a semi-
505 revolution it again came into contact with the stick, again slid up it,
506 and again bounded from it and fell over to the opposite side. This
507 movement of the shoot had a very odd appearance, as if it were
508 disgusted with its failure but was resolved to try again. (Darwin, 1875,
509 pp. 12-13)

510
511 We have observed similar surprising ways in which climbing plants sway away from
512 the regular elliptical revolution in a way that is congruent with the hypothesis that
513 the bean perceives the support and tries again and again by elongating to reach it.
514 Unfortunately, the videos where this movement is observed do not render
515 themselves to a rho/tau analysis since the coordinates cannot be extracted and
516 corrected with sufficient accuracy as to analyse them properly. One of our future
517 objectives is to perform a rho/tau analysis of the whole pattern of movement, from
518 original circumnutation all the way to the twining and securing of the support.
519

520 Conclusion

521 In *The movements and habits of climbing plants* Darwin observes:

522
523 It has often been vaguely asserted that plants are distinguished from
524 animals by not having the power of movement. It should rather be said
525 that plants acquire and display this power only when it is of some
526 advantage to them; this being of comparatively rare occurrence, as
527 they are affixed to the ground, and food is brought to them by the air
528 and rain. (p. 206).

529
530 We are now aware not only that plants' behaviour is reversible, non-automatic, and
531 repeatable in a manner that responds to metabolically salient features of the
532 environment (Calvo et al., 2014), but also of the increasing degree of sophistication
533 of plant movements as a function of the specific goal to be attained. Anthony
534 Trewavas considers the stilt palm (Allen, 1977), a plant whose light-foraging
535 behaviour results in the selective growing of new roots in the direction of sunlight,
536 letting the older ones die. Trewavas writes:

537
538 the filiform stem explores, locates and recognizes a new trunk and
539 reverses the growth pattern. As it climbs, the internode becomes
540 progressively thicker and leaves progressively redevelop to full size...
541 This behaviour is analogous to animals that climb trees to forage,

542 intelligently descend when food is exhausted or competition severe,
543 and then climb the next tree. (2003, p. 15)

544

545 Other strategies plants have evolved include the capacity to selectively becoming
546 mobile or sessile, alternatively, as a function of the environmental demands (Ray,
547 1992). Twining around a support is certainly not the only pattern of movement of
548 interest in the plant kingdom. We may thus wonder whether the ecological laws of
549 animal goal-directed movement apply to plants more generally. In fact, further
550 potential applications of general tau/rho theory to plants include analysing, for
551 instance, how orchid flowers orient to gravity (with their ‘chins’ down); shoots grow
552 up from an initial horizontal orientation; stems orient their flowers to light; root tips
553 guide their growth downward; root tips guide their growth away from light; etc.
554 Although more research is needed, the results reported here are consistent with an
555 ecological interpretation of the power of movement of plants.

556

557

558 **Acknowledgments**

559 This research was supported by Fundación Séneca-Agencia de Ciencia y Tecnología
560 de la Región de Murcia, through project 11944/PHCS/09 to PC and DL. We thank
561 Antonio Guirao for providing us with the perspective-error correction equations and
562 figures 1 and 2.

563

564 **Author contributions**

565 D.N.L. and P.C. conceived, designed the experiments, and wrote the paper. V.R.
566 digitized the time-lapse frames. P.C. and V.R. prepared the experimental set up at
567 MINT Lab, performed the experiments, and post-processed the data. D.N.L.
568 performed the rho/tau analysis.

569

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