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Motility and Gravitactic Orientation of the Flagellate, *Euglena gracilis*, Impaired by Artificial and Solar UV-B Radiation

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Abstract. The effects of ultraviolet radiation on the gravitactic orientation of the freshwater flagellate, *Euglena gracilis*, were determined by a real time image analysis system. Both artificial UV radiation and solar radiation in a temperature-controlled growth chamber were employed. Histograms of gravitaxis showed that the degree of orientation decreased with increasing exposure time; this can be quantified using the Rayleigh test and upper quadrant summation. The effects of artificial UV radiation on the orientation are considerably stronger than those of solar radiation, probably because the radiation source emits higher fluence rates below 300 nm than found in solar radiation. The effects of monochromatic ultraviolet radiation on motility have been determined, and an action spectrum has been calculated.

Like many other motile microorganisms, the photosynthetic unicellular flagellate, *Euglena gracilis*, orients in its habitat by a number of external chemical and physical parameters [37, 59]. Some motile microorganisms have been found to orient in the water column with the aid of chemical [5, 54] and thermal [57, 61] gradients, the magnetic field of the earth [24, 26, 60], and even electrical currents [56]. *Euglena* mainly orients with respect to light [18, 20, 43, 45, 53] and gravity [14, 34]. In addition to a weak photokinetic effect [76], both step-up and step-down photophobic responses [21, 22, 67] were characterized. However, the most important light responses are positive and negative phototaxis in this organism [43, 56].

The antagonism between positive phototaxis (strongly enhanced by negative gravitaxis, described below) and negative phototaxis causes the cells to accumulate in a band of suitable light conditions [38]. This behavior has important ecological consequences, not only for photosynthetic microorganisms, since cellular pigments are easily bleached by the bright light intensity at the surface of the water column [46, 47, 58, 62, 63]. Furthermore, the UV-B component of solar radiation has been found to affect both motility and photoorientation in *Euglena* [32, 33, 39, 40] and other photosynthetic and nonphotosynthetic microorganisms [31, 35, 41, 44].

Gravitaxis is the second important factor for orientation; it has the advantage of being available in the absence of light. Gravitactic orientation was observed more than a century ago [1, 49, 65, 73]. Recently, mainly ciliates [25, 48, 71] and flagellates have been studied [19, 50, 51, 63] in addition to a few other species [review in 4, 7–13, 17, 75].

Euglena shows an exclusive negative gravitaxis [34], which supports the less well pronounced positive phototaxis and takes the organisms to the surface of the water column. In contrast to higher plants, neither the cellular receptor nor the sensory transduction chain of the gravitactic orientation has been identified. It is still an open question whether graviorientation in flagellates is brought about by an active physiological perception or a passive physical process such as an asymmetric mass distribution [14, 52, 72].

In the ciliate *Paramecium*, Roberts [64] assumes a hydrodynamic interaction between the medium and the specific cell form to be the mechanism of gravitactic orientation, while another model tries to explain gravitaxis by a non-equilibrium ratio between sedimentation and rotation during propulsion [74]. Buoyancy is not the only source for negative gravitaxis [30], as has been shown by Taneda et al. [72], who also excluded an effect of the hydrostatic pressure [71]. The aim of this paper is to quantify

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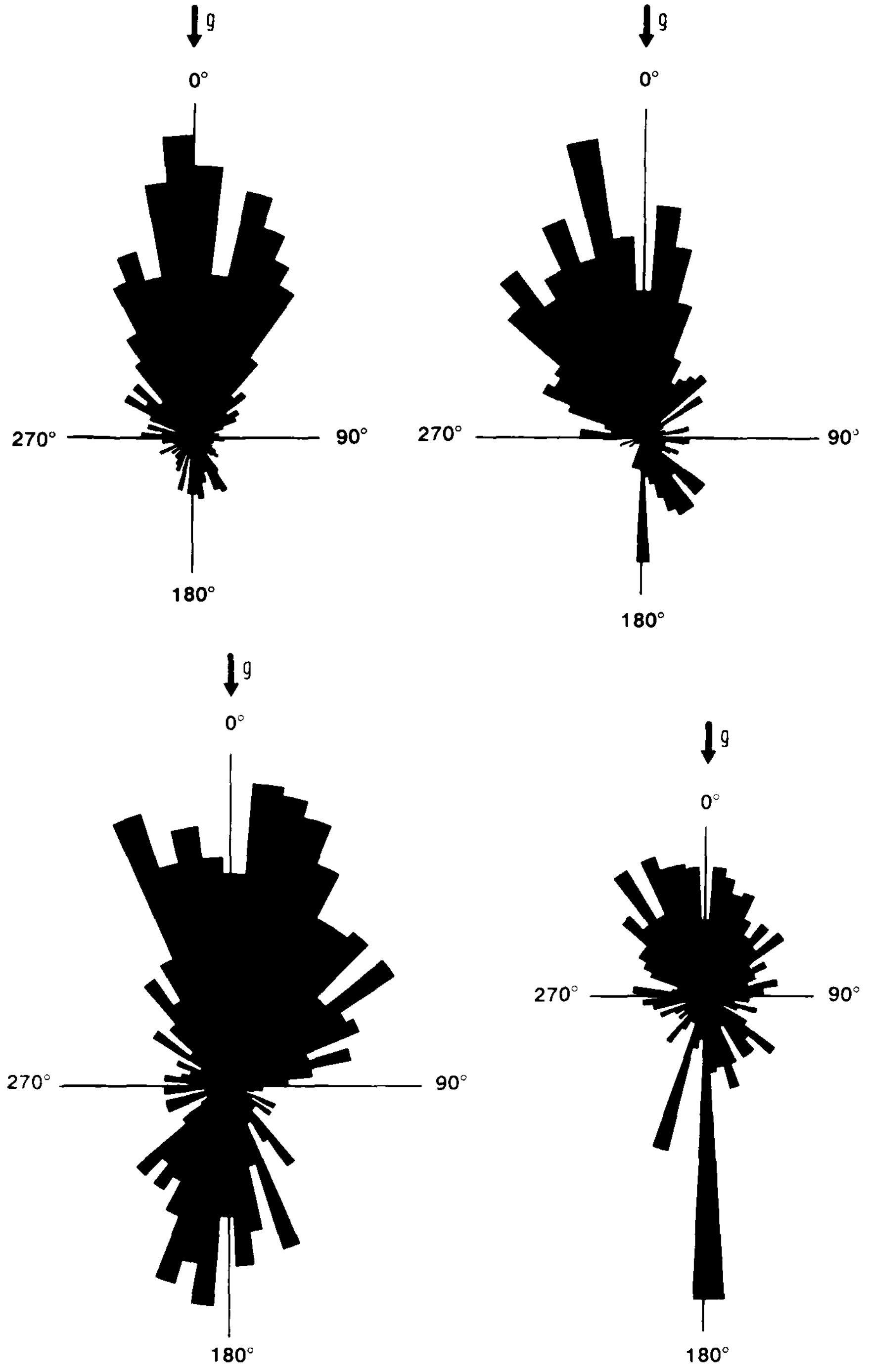

Fig. 1. Circular histograms of the movement direction of *Euglena gracilis* in a vertical cuvette after 0 min (a), 40 min (b), 70 min (c), and 130 min (d) of solar radiation. 1000 tracks were determined for each histogram and binned in 64 sectors. The arrows indicate the direction of the gravity vector.

and characterize the effects of solar and artificial ultraviolet radiation on the gravitactic orientation and motility in the freshwater alga, *Euglena gracilis*, and to determine an action spectrum for the UV effects.

Materials and Methods

Organism and culture. All experiments described in this article were performed with the freshwater flagellate, *Euglena gracilis*, strain Z. The cells were inoculated into 40 ml of a medium described recently [16, 69] contained in 100-ml Erlenmeyer flasks and grown for about 6 weeks under continuous light of about 600 lx (= 2.5 W m^{-2} from mixed cool white and warm-tone fluorescent lamps) at about 23°C. All experiments were carried out with the cells in their original growth medium. Cell suspensions were removed from the cultures and subjected to either artificial UV or solar irradiation.

Artificial UV irradiation. Ultraviolet irradiation was produced from a transilluminator (Bachofer, Reutlingen, FGR). The light

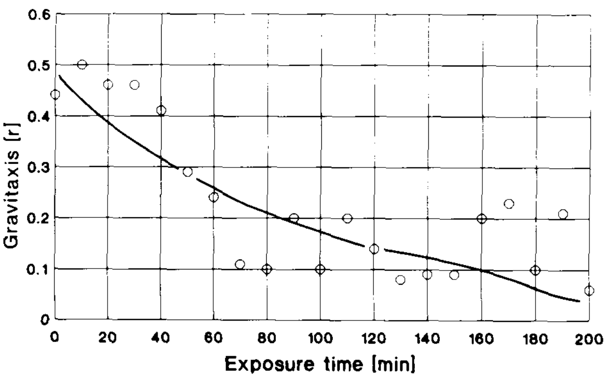

Fig. 2. Degree of gravitactic orientation (Rayleigh test, ordinate) of *Euglena gracilis* in a vertical cuvette in dependence on the exposure time to solar radiation (abscissa, min).

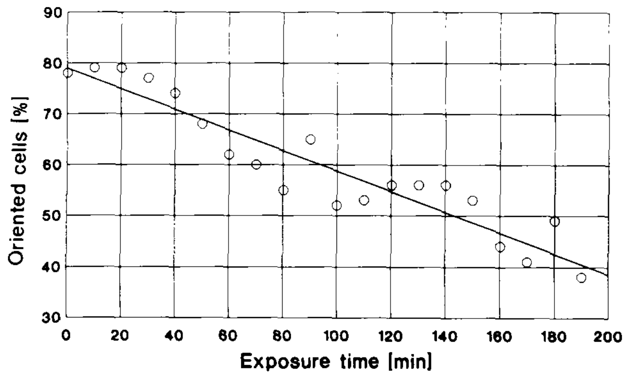

Fig. 3. Degree of gravitactic orientation of *Euglena gracilis* in a vertical cuvette in dependence on the exposure time to solar radiation (abscissa, min), quantified by calculating the percentage of cells moving in the upper two quadrants.

source emits very little visible light, and the radiation is higher than solar radiation below 300 nm and lower than solar radiation above 300 nm. The algal suspension was irradiated in an open glass cuvette (50 × 50 × 18 mm) covered with a 13% UV-B-transmitting, neutral density filter when placed under the inverted transilluminator. The effect of monochromatic ultraviolet radiation on motility in the flagellates was studied with a 900-W XBO xenon arc light source (Schoeffel LH 151) in combination with an Ebert type monochromator (Kratos GM 250) equipped with entrance and exit slits of 4 mm to give a halfband width of 8.2 nm. The grating had 1180 lines/mm blazed at 300 nm.

Solar irradiation. Cell suspensions were irradiated in open plastic Petri dishes, placed in a temperature-controlled (20°C) growth chamber (Weiss, Gießen, FRG) for solar exposure. The top of the growth chamber was made of Plexiglass, which transmitted >92% of the radiation between 280 nm and 700 nm. All experiments were carried out between 7. and 22. August, 1989, at a location south of Lissabon (Caparica, Portugal, 38° north) on sunny days between 10.30 h and 15.00 h local time. The fluence rates and spectral distributions were measured by Prof. Tevini and his coworkers (Karlsruhe, FRG) with a double monochromator spectroradiometer (Optronics model 742, Orlando, Florida). The total daily fluence of solar radiation in the UV-B range was about 67 kJ m^{-2}. At local noon the UV-B irradiation was about 2.0 W m^{-2} outside the growth chamber and about 1.96 W m^{-2} inside the growth chamber. Samples were taken at regular time intervals for gravitaxis measurements with the image analysis system.

Image analysis of motility and graviorientation. Gravitaxis of the flagellates was measured in darkness in a glass cuvette (75 × 8 × 0.17 mm^3 inner dimensions) placed on the stage of a horizontally oriented microscope (Zeiss Standard, Oberkochen, FRG). The microscope light beam was filtered through an infrared cut-off filter (RG 715, Schott & Gen., Mainz, FRG) to avoid phototaxis and photosynthetic effects by the monitoring light. A dark-field condensor was used to enhance the contrast, and the image of the moving cells was recorded by a CCD b/w camera (Philips LHD 0600) mounted on top of the microscope [36]. The video signal was digitized in real time (Matrox, PIP 1024, Quebec, Canada) with a spatial resolution of 512 × 512 pixels at 256 possible grey levels. An IBM AT compatible microcomputer (Tatung CS 8000, Taipei, Taiwan) had access to the image in memory.

The software package was written in the computer language C [42], but time critical calculations such as the determination of the outline and position of each organism were developed in Assembly language with the chain code algorithm [27–29]. The movement vectors of the cells were stored in the form of deviation angles from the gravity vector. The velocity of the organisms was calculated from the distance they had moved in the time determined from the hardware clock of the computer. Subsequent programs were developed to allow statistical and mathematical analysis such as the Rayleigh values and quadrant summation, which quantified the precision of orientation.

Results

In the absence of light, more than 75% of the cells of *Euglena gracilis* swam upwards to the top of the cuvette (Fig. 1a). The negative gravitactic orientation of the population was already slightly impaired after a short exposure (40 min) of the cells to solar radiation (Fig. 1a). After 70 min of solar radiation a considerable percentage of the cells moved downward, and the degree of orientation decreased significantly (Fig. 1c). After 130 min the cells were highly unoriented, and many cells were immotile and sedimented passively (Fig. 1d). Quantification of the degree of orientation using the Rayleigh test [2, 3, 55] indicated a drastic decrease even after short exposure times (Fig. 2). After about 70 min a residual value of about 0.15 was reached. Most cells, however, were still motile for up to 200 min. Also the quadrant calculation indicated an early effect of solar radiation on the degree of orientation (Fig. 3). After about 100 min the cells were randomly oriented, and after about 160 min a considerable fraction of all cells started to sediment passively.

Artificial ultraviolet radiation had similar effects on gravitactic orientation of the cells as solar radiation. The initial precise orientation of the cells with

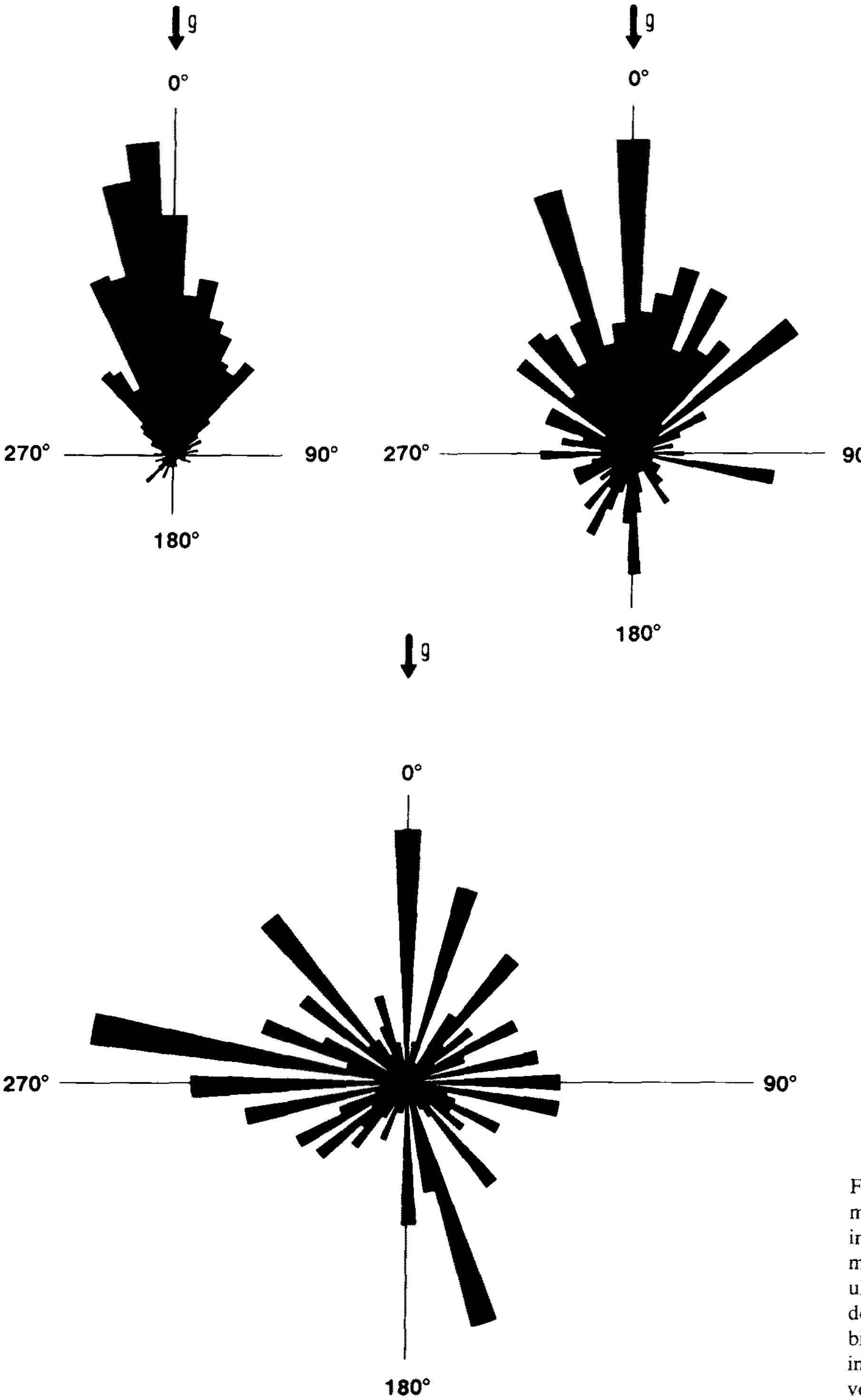

Fig. 4. Circular histograms of the movement direction of *Euglena gracilis* in a vertical cuvette after 0 min (a), 60 min (b), and 100 min (c) of artificial ultraviolet radiation. 1000 tracks were determined for each histogram and binned in 64 sectors. The arrows indicate the direction of the gravity vector.

an r-value of about 0.73 (Fig. 4a) was impaired after short exposure times, and after 60 min the degree of orientation had fallen to an r-value of 0.35 (Fig. 4b). After 100 min of ultraviolet radiation the still motile cells were completely unoriented (Fig. 4c), indicated by an r-value of 0.10. This tendency and the even faster inhibition of gravitactic orientation is quantified by plotting the r-values in dependence of the exposure time (Fig. 5), and also the quadrant calculation confirms the fast effect of artificial ultraviolet radiation (Fig. 6).

For an action spectrum of ultraviolet radiation on the motility of *Euglena gracilis*, the effects of monochromatic radiation were determined at

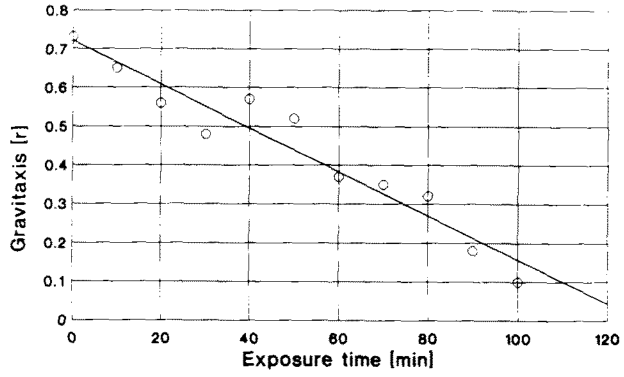

Fig. 5. Degree of gravitactic orientation (Rayleigh test, ordinate) of *Euglena gracilis* in a vertical cuvette in dependence on the exposure time to artificial ultraviolet radiation (abscissa, min).

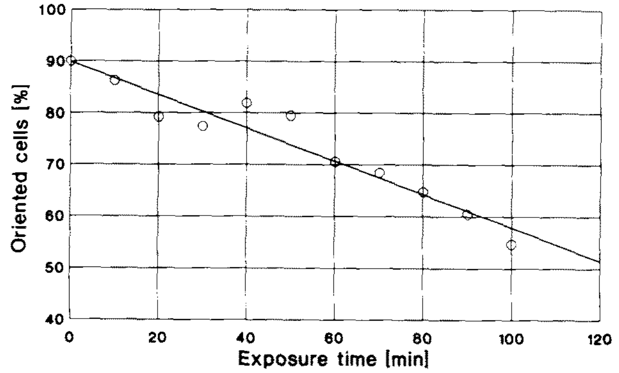

Fig. 6. Degree of gravitactic orientation of *Euglena gracilis* in a vertical cuvette in dependence on the exposure time to artificial ultraviolet radiation (abscissa, min), quantified by calculating the percentage of cells moving in the upper two quadrants.

wavelengths in the ultraviolet range (Fig. 7). The action spectrum calculated from these curves has a major maximum at about 270 nm, a shoulder at 290 nm, and a secondary maximum at about 305 nm (Fig. 8). The spectral distribution of solar radiation has been calculated for a location at about 50° north with a computer simulation program [6]. Comparison of the two curves indicates which parts of the action spectrum are ecologically significant.

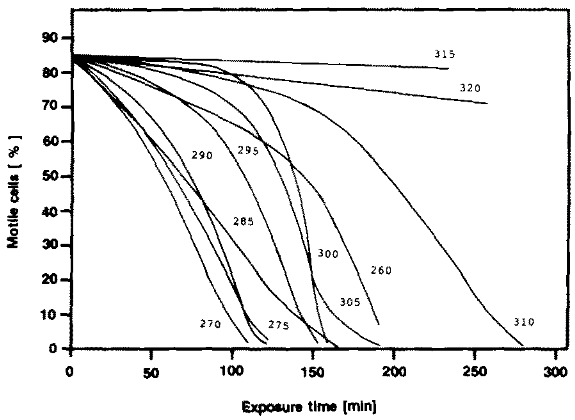

Fig. 7. Dependence of the percentage of motile cells in *Euglena gracilis* on the exposure time to monochromatic ultraviolet radiation (wavelengths indicated at the curves).

Discussion

Gravitaxis in *Euglena gracilis* is significantly impaired by exposure to solar radiation and artificial UV. The inhibition of gravitactic orientation by artificial UV irradiation supports the notion that the effects of solar radiation are due mainly to the UV component rather than to visible light. Thermal effects can be excluded for both solar and artificial radiation. However, an additional white light effect may be involved in solar radiation, because long-term white light irradiation at high fluence rates had been found to impair pigment composition and survival of Dinoflagellates and Cryptophyceae [23, 47].

The inhibition of gravitaxis in *Euglena gracilis* is independent of the decrease in motility; this finding supports the hypothesis that the process of gravi-orientation may be the result of an active perception rather than a passive physical effect such as an asymmetric position of the center of gravity. After a prolonged exposure to ultraviolet irradiation, many cells move downwards in the water column both by active swimming and by passive sedimentation. This may be an effective mechanism to escape from the detrimental UV irradiation at the surface.

The action spectrum of ultraviolet irradiation effects on motility differs remarkably from those involving DNA as the primary UV target [66, 70]. It also differs from the generalized plant action spectrum for UV-B effects [15]. Damage of DNA by ultraviolet irradiation has been excluded as a possible mechanism for inhibition of motility in *Euglena gracilis* on the basis of a lack of photorepair and the short effective exposure times [39]; moreover, photodynamic responses were excluded because specific quenchers and scavengers of singlet oxygen and free radicals were not effective [40]. The action spectrum supports the hypothesis that an intrinsic component of the motor apparatus, such as a flagellar protein, is the primary target of detrimental ultraviolet irradiation.

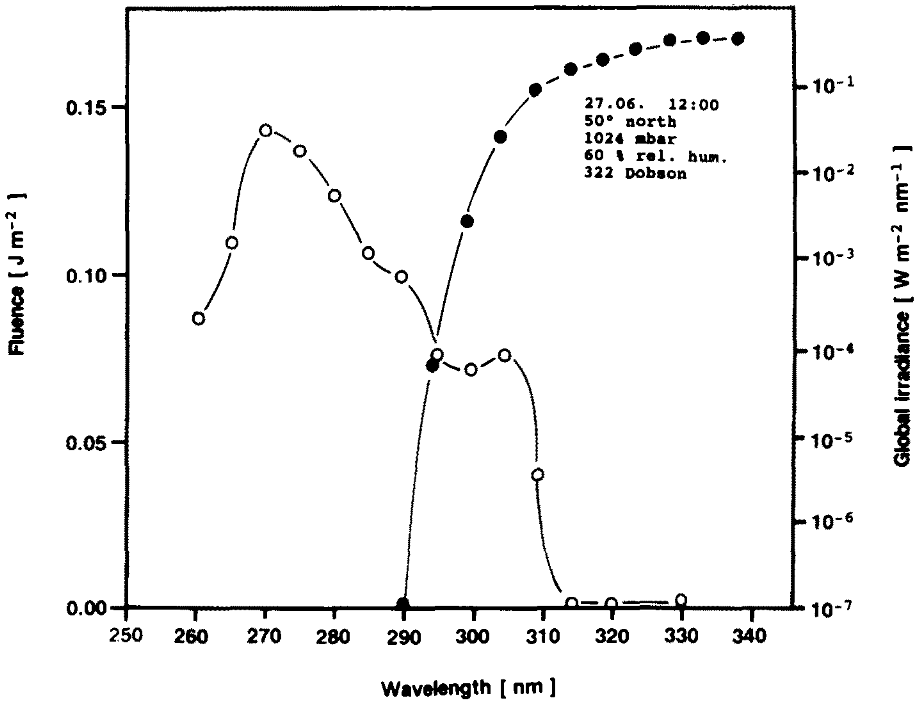

Fig. 8. Action spectrum of the effects of ultraviolet radiation on the percentage of motile cells in *Euglena gracilis*. For comparison, the spectral distribution of solar radiation at a location 50° north (Erlangen) is inserted for June 27, local noon.

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Literature Cited

1. Aderhold R (1988) Beiträge zur Kenntnis richtender Kräfte bei der Bewegung niederer Organismen. Jen Z Med Naturwiss 22:311–342
2. Batschelet E (1965) Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. In: Galles SR, Schmidt-Koenig K, Jacobs GJ, Belleville RF (eds) Animal orientation and navigation. Washington: NASA, pp 61–91
3. Batschelet E (1981) Circular statistics in biology. London: Academic Press
4. Bean B (1984) Microbial geotaxis. In: Colombetti G, Lenci F (eds) Membranes and sensory transduction. New York, London: Plenum Press, pp 163–198
5. Berg HC (1985) Physics of bacterial chemotaxis. In: Colombetti G, Lenci F, Song P-S (eds) Sensory perception and transduction in aneural organisms. New York, London: Plenum Press, pp 19–30
6. Björn LO, Murphy TM (1985) Computer calculation of solar ultraviolet radiation at ground level. Physiol Veg 23:555–561
7. Block J, Briegleb W, Sobick V, Wohlfarth-Bottermann KE (1986) Confirmation of gravisensitivity in the slime mold *Physarum polycephalum* under near weightlessness. Adv Space Res 6:143–150
8. Briegleb W (1984) Acceleration reactions of cells and tissues—their genetic-phylogenic implications. Adv Space Res 4:5–7
9. Briegleb W (1988) Ground-borne methods and results in gravitational cell biology. Physiologist 31:44–47
10. Briegleb W, Block I (1986) Classification of gravity effects on "free" cells. Adv Space Res 6:15–19
11. Briegleb W, Schatz A (1980) Changes of periodic protoplasmic movements on the fast clinostat. The Physiologist 23:137–138
12. Briegleb W, Schatz A (1980) Changes of periodic protoplasmic movements on the fast clinostat. Adv Physiol Sci 19:261–264
13. Briegleb W, Neubert J, Schatz A, Hordinsky JR, Cogoli A (1982) Cell morphological, ontogenic, and genetic reactions to 0-g simulation and hyper-g. Acta Astronautica 9:47–50
14. Brinkmann K (1968) Keine Geotaxis bei Euglena. Z Pflanzenphysiol 59:12–16
15. Caldwell MM (1971) Solar ultraviolet radiation and the growth and development of higher plants. In: Giese AC (ed) Photophysiology. New York: Academic Press, pp. 131–177
16. Checcucci A, Colombetti G, Ferrara R, Lenci F (1976) Action spectra for photoaccumulation of green and colorless Euglena: evidence for identification of receptor pigments. Photochem Photobiol 23:51–54
17. Cogoli A, Valluchi M, Reck J, Müller M, Briegleb W, Cordt I, Michel C (1979) Human lymphocyte activation is depressed at low-g and enhanced at high-g. The Physiologist 22:29–30
18. Colombetti G, Häder D-P, Lenci F, Quaglia M (1982) Phototaxis in Euglena gracilis: effect of sodium azide and triphenylmethyl phosphonium ion on the photosensory transduction chain. Curr Microbiol 7:281–284
19. Creutz C, Diehn B (1976) Motor responses to polarized light and gravity sensing in Euglena gracilis. J Protozool 23:552–556

20. Diehn B, Feinleib M, Haupt W, Hildebrand E, Lenci F, Nultsch W (1977) Terminology of behavioral response of motile microorganisms. Photochem Photobiol 26:559–560
21. Doughty MJ, Diehn B (1983) Photosensory transduction in the flagellated alga, *Euglena gracilis*. IV. Long-term effects of ions and pH on the expression of step-down photobehavior. Arch Microbiol 134:204–207
22. Doughty MJ, Diehn B (1984) Anion sensitivity of motility and step-down photophobic responses of *Euglena gracilis*. Arch Microbiol 138:329–332
23. Ekelund N, Häder D-P (1988) Photomovement and photobleaching in two *Gyrodinium* species. Plant Cell Physiol 29:1109–1114
24. Esquivel DMS, de Barros HGPL (1986) Motion of magnetotactic microorganisms. J Exp Biol 121:153–163
25. Fenchel T, Finlay BJ (1986) Photobehavior of the ciliated protozoon Loxodes: taxic, transient, and kinetic responses in the presence and absence of oxygen. J Protozool 33:139–145
26. Frankel RB (1984) Magnetic guidance of organisms. Annu Rev Biophys Bioeng 13:85–103
27. Freeman H (1961) On the encoding of arbitrary geometric configurations. IRE Trans EC-10:260–268
28. Freeman H (1974) Computer processing of line-drawing images. Comput Surv 6:57–97
29. Freeman H (1980) Analysis and manipulation of lineal map data. Map data processing. New York: Academic Press, pp 151–168
30. Fukui K, Asai H (1985) Negative geotactic behavior of *Paramecium caudatum* is completely described by the mechanism of buoyancy-oriented upward swimming. Biophys J 47:479–482
31. Häder D-P (1984) Effects of UV-B on motility and photoorientation in the cyanobacterium, *Phormidium uncinatum*. Arch Microbiol 140:34–39
32. Häder D-P (1985) Effects of UV-B on motility and photobehavior in the green flagellate, *Euglena gracilis*. Arch Microbiol 141:159–163
33. Häder D-P (1986) Effects of solar and artificial UV irradiation on motility and phototaxis in the flagellate, *Euglena gracilis*. Photochem Photobiol 44:651–656
34. Häder D-P (1987) Polarotaxis, gravitaxis and vertical phototaxis in the green flagellate, *Euglena gracilis*. Arch Microbiol 147:179–183
35. Häder D-P (1987) Effects of UV-B irradiation on photomovement in the desmid, *Cosmarium cucmis*. Photochem Photobiol 46:121–126
36. Häder D-P (1988) Computer-assisted image analysis in biological sciences. Proc Indian Acad Sci (Plant Sci) 98:227–249
37. Häder D-P (1988) Ecological consequences of photomovement in microorganisms. J Photochem Photobiol B: Biol 1:385–414
38. Häder D-P, Griebenow K (1988) Orientation of the green flagellate, *Euglena gracilis*, in a vertical column of water. FEMS Microbiol Ecol 53:159–167
39. Häder D-P, Häder M (1988) Ultraviolet-B inhibition of motility in green and dark bleached *Euglena gracilis*. Curr Microbiol 17:215–220
40. Häder D-P, Häder MA (1988) Inhibition of motility and phototaxis in the green flagellate, *Euglena gracilis*, by UV-B radiation. Arch Microbiol 150:20–25
41. Häder D-P, Häder MA (1989) Effects of solar UV-B irradiation on photomovement and motility in photosynthetic and colorless flagellates. Environ Exp Bot 29:273–282
42. Häder D-P, Vogel K (1990) Simultaneous tracking of flagellates in real time by image analysis. J Math Biol, in press
43. Häder D-P, Colombetti G, Lenci F, Quaglia M (1981) Phototaxis in the flagellates, *Euglena gracilis* and *Ochromonas danica*. Arch Microbiol 130:78–82
44. Häder D-P, Watanabe M, Furuya M (1986) Inhibition of motility in the cyanobacterium, *Phormidium uncinatum*, by solar and monochromatic UV irradiation. Plant Cell Physiol 27:887–894
45. Häder D-P, Lebert M, DiLena MR (1986) New evidence for the mechanism of phototactic orientation of *Euglena gracilis*. Curr Microbiol 14:157–163
46. Häder D-P, Rhiel E, Wehrmeyer W (1987) Phototaxis in the marine flagellate *Cryptomonas maculata*. J Photochem Photobiol 1:115–122
47. Häder D-P, Rhiel E, Wehrmeyer W (1988) Ecological consequences of photomovement and photobleaching in the marine flagellate *Cryptomonas maculata*. FEMS Microbiol Ecol 53:9–18
48. Hemmersbach-Krause R (1988) Vergleichende Untersuchungen zur Gravitaxis und zur Morphologie von *Loxodes* und *Paramecium*. Forschungsbericht der deutschen Forschungs- und Versuchsanstalt für Luft- und Raumfahrt 88-27:1–155
49. Jensen P (1983) Über den Geotropismus niederer Organismen. Pflüger's Arch ges Phys 53:428–480
50. Kessler JO (1985) Hydrodynamic focusing of motile algal cells. Nature 313:218–220
51. Kessler JO (1986) The external dynamics of swimming microorganisms. In: Round FE, Chapman DJ (eds) Progress in phycological research. Biopress Ltd. 4, pp 258–307
52. Kuroda K, Kamiya NMJA, Yoshimoto Y, Hiramoto Y (1986) *Paramecium* behavior during video centrifuge-microscopy. Proc Japan Acad 62, Ser B:117–121
53. Lenci F, Colombetti G, Häder D-P (1983) Role of flavin quenchers and inhibitors in the sensory transduction of the negative phototaxis in the flagellate, *Euglena gracilis*. Curr Microbiol 9:285–290
54. MacNab RM (1985) Biochemistry of sensory transduction in bacteria. In: Colombetti G, Lenci F, Song P-S (eds) Sensory perception and transduction in aneural organisms. New York, London: Plenum Press, pp 31–46
55. Mardia KV (1972) Statistics of directional data. London: Academic Press
56. Mast SO (1911) Light and behavior of organisms. New York: John Wiley & Sons
57. Mizuno T, Maeda K, Imae Y (1984) Thermosensory transduction in *Escherichia coli*. In: Oosawa F, Yoshioka T, Hayashi H (eds) Transmembrane signaling and sensation. Tokyo: Japan Sci Soc Press and VNU Sci Press BV, Netherlands, pp 147–195
58. Nultsch W, Agel G (1986) Fluence rate and wavelength dependence of photobleaching in the cyanobacterium *Anabaena variabilis*. Arch Microbiol 144:268–271
59. Nultsch W, Häder D-P (1988) Photomovement in motile microorganisms. II. Photochem Photobiol 47:837–869
60. Ofer S, Nowik I, Bauminger ER, Papaefthymiou GC, Frankel RB, Blakemore RP (1984) Magnetosome dynamics in magnetotactic bacteria. J Biophys 46:57–64
61. Poff KL (1985) Temperature sensing in microorganisms. In: Colombetti G, Lenci F, Song P-S (eds) Sensory perception and transduction in aneural organisms, New York, London: Plenum Press, pp 299–307
62. Rhiel E, Häder D-P, Wehrmeyer W (1988) Photo-orientation in a freshwater *Cryptomonas* species. J Photochem Photobiol B: Biol 2:123–132
63. Rhiel E, Häder D-P, Wehrmeyer W (1988) Diaphototaxis and

gravitaxis in a freshwater *Cryptomonas*. Plant Cell Physiol 29:755–760
64. Roberts AM (1970) Geotaxis in motile micro-organisms. J Exp Biol 53:687–699
65. Schwarz F (1884) Der Einfluß der Schwerkraft auf die Bewegungsrichtung von Chlamydomonas und Euglena. Dtsch Bot Ges 2:57–72
66. Setlow RB (1974) The wavelengths in sunlight effective in producing skin cancer: a theoretical analysis. Proc Natl Acad Sci 71:3363–3366
67. Shimmen T (1981) Quantitative studies on step-down photophobic response of *Euglena* in an individual cell. Protoplasma 106:37–48
68. Sobick V, Briegleb W, Block I (1983) Is there an orientation of the nuclei in microplasmodia of *Physarum polycephalum*? Physiologist 26:129–130
69. Starr RC (1964) The culture collection of algae at Indiana University. Am J Bot 51:1013–1044
70. Sterenborg HJCM, van der Leun JC (1987) Action spectra for tumorigenesis by ultraviolet radiation. In: Passchier WF, Bosujakovic BFM (eds) Human exposure to ultraviolet radiation: risks and regulations. Amsterdam: Elsevier Science Publishers, pp 173–190
71. Taneda K (1987) Geotactic behavior in *Paramecium caudatum*. I. Geotaxis assay of individual specimen. Zool Sci 4:781–788
72. Taneda K, Miyata S, Shiota A (1987) Geotactic behavior in *Paramecium caudatum*. II. Geotaxis assay in a population of the specimens. Zool Sci 4:789–795
73. Verworn M (1889) Die polare Erregung der Protisten durch den galvanischen Strom. Pflüger's Arch Physiol 45:1–36
74. Winet H, Jahn TL (1974) Geotaxis in protozoa: I. A propulsion-gravity model for Tetrahymena (Ciliata). J Theor Biol 46:449–455
75. Wolke A, Niemeyer F, Achenbach F (1987) Geotactic behavior of the acellular myxomycete *Physarum polycephalum*. Cell Biol Int Rep 11:525–528
76. Wolken JJ, Shin E (1958) Photomotion in *Euglena gracilis*. I. Photokinesis. II. Phototaxis. J Protozool 5:39–46