

Corrections

BIOPHYSICS AND COMPUTATIONAL BIOLOGY, ASTRONOMY

Correction for “Detection of circular polarization in light scattered from photosynthetic microbes,” by William B. Sparks, James Hough, Thomas A. Germer, Feng Chen, Shiladitya DasSarma, Priya DasSarma, Frank T. Robb, Nadine Manset, Ludmilla Kolokolova, Neill Reid, F. Duccio Macchetto, and William Martin, which appeared in issue 19, May 12, 2009, of *Proc Natl Acad Sci USA* (106:7816–7821; first published April 28, 2009; 10.1073/pnas.0810215106).

The authors note that due to a printer’s error, in Fig. 1 on page 7817, ports A, B, and C were not labeled. The corrected figure appears below.

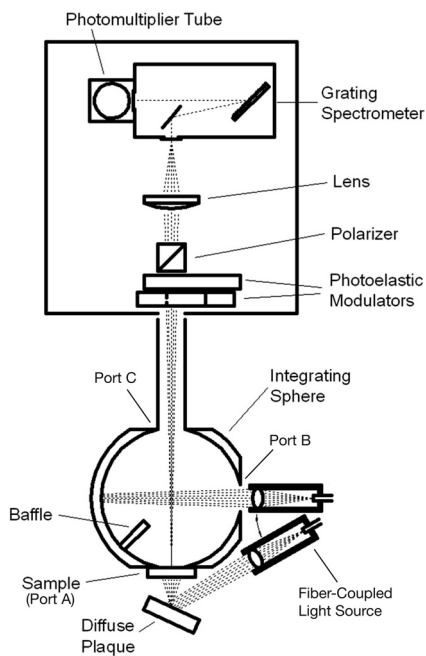


Fig. 1. Illustration of the experimental configuration. In reflection mode, the light from a fiber-coupled quartz-tungsten-halogen lamp enters through an open port (B) into a 200-mm diameter integrating sphere, illuminating a spot on the sphere wall opposite. A baffle is located between the illuminated spot and the sample at port A to reduce direct illumination from that direction. The light is depolarized by numerous internal reflections and exits as unpolarized diffuse light onto the surface of the sample at port A. The polarimeter views the sample from the surface normal at port C and the sample at port A is imaged onto the entrance slit of the monochromator. In transmission mode, the horizontal port B is closed and the same light source is used to illuminate a diffuse white plaque beneath the sample and this low-polarization white light passes through the sample directly to the polarimeter.

www.pnas.org/cgi/doi/10.1073/pnas.09054001106

MEDICAL SCIENCES

Correction for “Sjögren’s syndrome-like disease in mice with T cells lacking class 1A phosphoinositide-3-kinase,” by Jean S. Oak, Jonathan A. Deane, Michael G. Kharas, Ji Luo, Thomas E. Lane, Lewis C. Cantley, and David A. Fruman, which appeared in issue 45, November 7, 2006, of *Proc Natl Acad Sci USA* (103:16882–16887; first published October 27, 2006; 10.1073/pnas.0607984103).

The authors note that in Fig. 5A on page 16885, the labels IL-10 and IL-2 were switched. The corrected figure appears below.

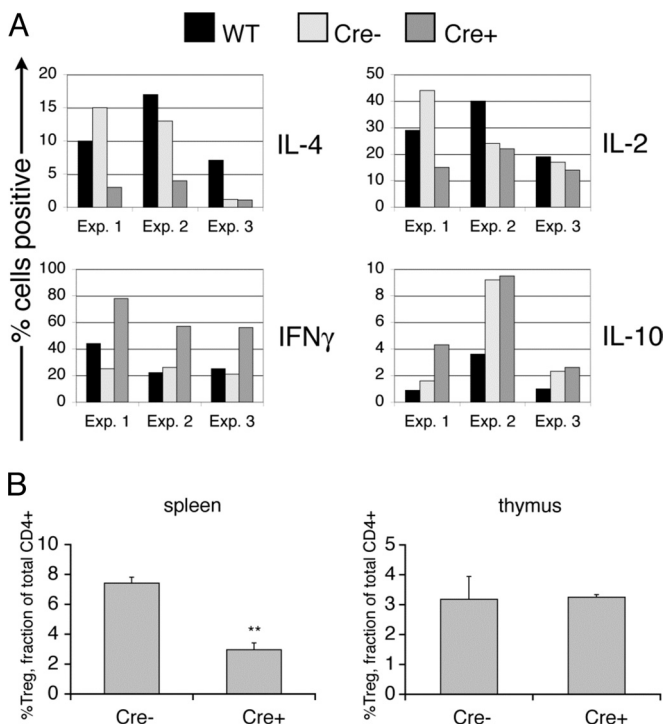


Fig. 5. *r1ΔT/r2n* mice show altered T helper differentiation and decreased regulatory T cell frequency. (A) Defective differentiation in *r1ΔT/r2n* CD4⁺ T cells after activation and expansion under Th2 polarizing conditions. Effector CD4⁺ T cells of the indicated genotypes were restimulated with phorbol 12-myristate 13-acetate plus ionomycin, and the percentages of cells secreting the indicated cytokines were enumerated by intracellular staining. Th2 skewing is generally incomplete in this mixed genetic background (129SvEv × C57BL/6), as in C57BL/6 and related inbred strains. (B) Six- to 8-week-old *r1ΔT/r2n* mice have a significant reduction ($P < 0.01$) in the percentage of CD4⁺CD25⁺FoxP3⁺ peripheral Treg cells in the spleen (Left) but not the thymus (Right).

www.pnas.org/cgi/doi/10.1073/pnas.09054011106

Detection of circular polarization in light scattered from photosynthetic microbes

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The identification of a universal biosignature that could be sensed remotely is critical to the prospects for success in the search for life elsewhere in the universe. A candidate universal biosignature is homochirality, which is likely to be a generic property of all biochemical life. Because of the optical activity of chiral molecules, it has been hypothesized that this unique characteristic may provide a suitable remote sensing probe using circular polarization spectroscopy. Here, we report the detection of circular polarization in light scattered by photosynthetic microbes. We show that the circular polarization appears to arise from circular dichroism of the strong electronic transitions of photosynthetic absorption bands. We conclude that circular polarization spectroscopy could provide a powerful remote sensing technique for generic life searches.

homochirality | life detection | remote sensing

The search for life in the Universe depends on the identification of observable signatures that are unique to biological processes. If these signatures may be sensed remotely, then extensive surveys of planetary surfaces and distant objects may be undertaken without the need (initially) for costly landing spacecraft. A candidate universal biosignature that may lend itself to remote sensing application is homochirality, which, because of the optical activity of biological molecules, is potentially detectable using circular polarization spectroscopy (1–6). Organic molecules typically exist in 2 mirror-image forms and are said to be “chiral”; that is, they exhibit handedness. All known living organisms use only left-handed or l-amino acids in proteins and right-handed or d-sugars in nucleic acids and this unique preference for just a single handedness is termed “homochirality.” Intriguingly, analysis of the Murchison meteorite has shown l-excesses of 2–9% for a number of α -methyl amino acids (7), with slightly smaller excesses found in the Murray meteorite (8). Homochirality is thought to be generic to all forms of biochemical life as a necessity for self-replication (9) and hence it is likely to be a signature of nonterrestrial life. To be detectable remotely using circular polarization, homochirality must imprint itself upon the circular polarization spectrum in scattered light. Here, we report on the results of sensitive laboratory measurements of the polarization spectra of light both scattered from photosynthetic microbes and in transmission through the same cultures. For context, we also present polarization spectra of a leaf and a mineral.

There is a vast array of experimentation that may be brought to bear in the case of in situ tests for the presence of biological processes (10); however, in situ experiments can sample only a tiny fraction of a planetary surface and its immediate subsurface, and they often anticipate a degree of specificity in the biology sought. Few remote sensing methods directly probe signatures of biological life. Trace gases can be observed that could have a biological origin, such as recent detections of localized methane production on Mars (11). Jupiter’s moon Europa is strongly suspected to host a liquid water ocean (12), and infrared

spectroscopic features have been shown to be consistent with those of radiation tolerant microbes (13). Beyond the Solar System, methods will be needed to assess whether extrasolar planets harbor life, and remote sensing is a necessity. Attention is being given to atmospheric composition disequilibria and to biological pigmentation spectral features as biomarkers (14–16). Typical disadvantages of these methods include model dependence and the possibility that the “biosignature” could be produced by abiotic processes, leading to a false positive.

Circular polarization may provide a more direct indication of the presence of biological processes because it is directly attributable to the chirality of the organic molecules. Earlier experiments (1, 3, 4) looked at leaves and found significant circular polarization. Here, we focus on light reflected from photosynthetic bacterial cultures. Photosynthetic life must reside at the surface, use windows of atmospheric transparency and exploit regions of the spectrum where the host star shines brightly, and hence such life forms are maximally observable. The strong electronic absorption bands that are characteristic of photosynthesis are known to exhibit circular dichroism (different absorption coefficients for left- and right-circularly polarized light); hence, we may anticipate a consequent polarization signature in scattered light, although because of the complexities of the scattering process, this is not entirely obvious in advance. For example, multiple scattering tends to randomize the polarization state; or alternatively, any circular polarization produced in the incident direction might be cancelled by circular polarization produced by subsequent reflection, because this will have the opposite handedness. If the scatterers depolarize the light, then an appropriate balance between the scattering coefficient and the differential absorption coefficient is needed to achieve measurable circular polarization. In this work, we are testing whether that balance can be achieved with microorganisms. Circular polarization can also be caused by optical interaction associated with the chirality of subcellular structures, such as membranes and macromolecules, aspects that clearly relate to the presence of biology, although yielding a distinct spectral signature relative to the circular dichroism of absorption bands (17).

Photosynthetic cyanobacteria arose between 2 and 3 billion years ago (18, 19). The enormous evolutionary advantages of photosynthesis coupled to the resilience of these microbes led to planet-wide changes in the demographic abundance of terrestrial life forms and in turn, to major changes in the composition of the

Author contributions: W.B.S., J.H., T.A.G., and N.M. designed research; W.B.S., J.H., T.A.G., F.C., S.D., P.D., F.T.R., N.M., L.K., N.R., F.D.M., and W.M. performed research; F.C., S.D., P.D., and F.T.R. contributed new reagents/analytic tools; W.B.S., T.A.G., and N.M. analyzed data; and W.B.S., J.H., T.A.G., F.C., S.D., P.D., F.T.R., N.M., L.K., N.R., F.D.M., and W.M. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

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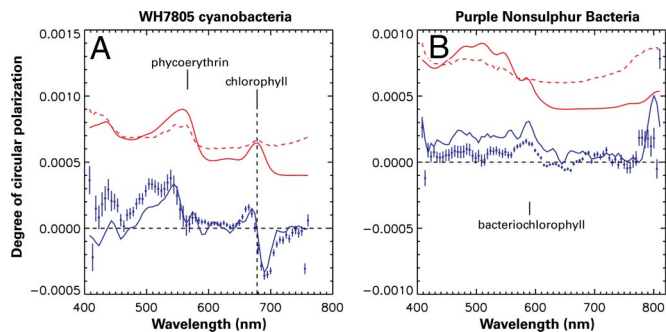


Fig. 3. Polarization spectra of cyanobacteria WH7805 and of purple nonsulfur bacteria *R. rubrum*. (A) Both transmission and reflection polarization spectra of cyanobacteria *Synechococcus* WH7805. Transmission is shown as a solid blue line, and reflection with solid blue circles and error bars. Note the high degree of similarity between the two. The solid red line shows a scaled $-\log_{10}(\text{Reflectance})$ spectrum and the dashed red line a scaled plot of the degree of linear polarization. (B) Similarly shows transmission, solid blue line, and reflection, blue dots, polarization spectra for purple nonsulfur bacteria *R. rubrum*. The red solid line shows a scaled $-\log_{10}(\text{Reflectance})$ spectrum and the red dashed line a scaled plot of the degree of linear polarization. Bacteriochlorophyll has absorption peaks at ≈ 590 nm and 800 nm, which appear in these data.

The reflection experiment for WH8101 (Fig. 2B) shows reflectance and polarization spectra that very closely mimic the transmission experiment. (The reflectance is proportional to the square of the transmittance, expected given the double pass through the material.) The circular polarization reflection spectrum shows all of the same features as the transmission polarization spectrum, even though the sample was illuminated with unpolarized light. We see the blue-absorbing carotenoids, the phycocyanin antenna pigment and the chlorophyll *a* dimer conservative circular polarization sign change. The amplitude of polarization is similar for transmission and reflection spectra. The presence of the circular polarization sign change at 680 nm is a very strong indication that we are witnessing the molecular circular dichroism of the material even in the scattered light spectrum.

WH7805 (Fig. 3A) exhibits very similar behavior, with the antenna pigment phycoerythrin absorption at ≈ 550 nm replacing the 620-nm phycocyanin band. As before, circular polarization is present, associated with these absorption bands, including the distinctive sign change for chlorophyll. Again, the essential characteristics of the circular polarization transmission spectrum are fully reproduced in the polarization spectrum of reflected light, also shown in Fig. 3A. Likewise, Fig. 3B, the polarization reflection and transmission spectra of *R. rubrum* are similar to one another and show circular polarization associated with bacteriochlorophyll absorption at ≈ 590 nm and blue absorbing carotenoid chromophores.

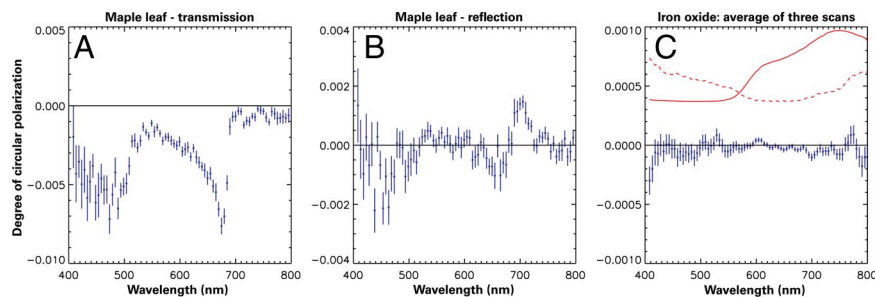


Fig. 4. Circular polarization spectra for a leaf and a mineral. (A) A maple leaf transmission polarization spectrum. (B) Corresponding maple leaf reflection polarization spectrum. (C) A control iron oxide polarization spectrum. The blue data points with error bars are the degree of circular polarization in each image. The solid red line in C shows the reflection spectrum of iron oxide, and the dashed red line shows the degree of linear polarization, both arbitrarily scaled.

For context, Fig. 4A and B shows polarization spectra of a fresh green maple leaf. The transmission spectrum shows very strong circular polarization, largely mimicking chlorophyll *a* molecular circular dichroism. The reflected circular polarization spectrum also shows a strong chlorophyll *a* 680-nm polarization signature, with an accompanying sign change through the absorption maximum. Curiously, the sign is reversed with respect to the cyanobacteria, which we speculate is due to the more complex leaf optics.

Fig. 4C shows the polarization of red iron oxide powder, chosen because it has a spectral edge not unlike chlorophyll and might present a false positive in a chlorophyll red-edge detection experiment. The sample also serves to guard against potential instrumental effects that might have been associated with strong spectral features (none were found). The spectropolarization signature of the iron oxide is very close to the noise limit of the instrument; there is a lack of any pronounced spectral features in circular polarization, and there is no correlation with the absorption spectrum. Likewise, Pospergelis (1) showed circular spectropolarimetry of a variety of other minerals with similar results. These characteristics are quite different to those of the biological samples.

Discussion

Scattered light microbial polarization levels are in the range $p_c \approx 10^{-3}$ to 10^{-4} , the leaf has $p_c \approx 2 \times 10^{-3}$, whereas the iron oxide has a root mean square noise level $p_c \approx 4 \times 10^{-5}$, where p_c is the degree of circular polarization, which lies between 0 and 1 (see *Materials and Methods*). Good astronomical polarimeters (32) can measure polarization degree $p_c \approx 10^{-6}$, although high light levels are required. Hence, the tolerance to dilution of a biological polarization signal from the many potential sources of unpolarized light that can enter the field of view of a practical remote sensing experiment is a factor ≈ 10 –100. For example, in arid desert environments, rocks and sand will dilute spectral features and polarization degree with unpolarized light, hence contiguous microbial colonies could be detectable if they contribute 1–10% or more of the light from the viewing scene. By contrast if a material is undiluted but only partially chiral, the spectral absorption band will remain at its full strength whereas the polarization signature is diluted because of the incomplete homochirality. (If modest chiral excesses can be found somewhere beyond the Earth, and recognized by comparison of the their spectra to their polarization spectra, this would be of great interest to scientists studying the origin of life and origin of homochirality.)

Concerning the possibility of false positives, initial circular polarization imaging of the Mars surface (6) did not yield any significant signatures, which is encouraging in that false positives were not found to be abundant. Laboratory measurements of minerals, including here, have consistently revealed polarization

PEMs, using a digital signal processor, whereas the circular Stokes parameter, V , is measured by the 1f modulation frequency of the first PEM, using a lock-in amplifier for additional precision. The DC component provides the total intensity I . The degree of circular polarization in the presence of fully linearly polarized light was zero within our confidence of being able to generate fully linearly polarized light. The polarimeter is tunable from 400 nm to 800 nm and is controlled automatically by software that establishes scans across a selected wavelength range in discrete steps with a specified dwell time at each wavelength. The monochromator has a spectral resolution of ≈ 15 nm FWHM, which we most commonly sample with 5-nm step sizes.

Microbial and Control Samples. Unicellular cyanobacteria of the genus *Synechococcus* are among the most abundant members of the picophytoplankton, which can contribute up to 30% of primary production in the surface waters of world's oceans (20, 21). The *Synechococcus* group (Chroococcales) is a provisional assemblage loosely defined as unicellular coccoid to rod-shaped cyanobacteria, $<3 \mu\text{m}$ in diameter. Many strains have been isolated from freshwater, estuarine, coastal and oceanic waters (23). Cyanobacteria uniquely contain phycobilisome light harvesting accessory pigments, PC and PE. The PC rich *Synechococcus* dominate in coastal estuary, PE rich *Synechococcus* in the open ocean. Strains WH8101 and WH7805 represent 2 such picocyanobacteria (21). WH8101 was originally isolated from the pier of Woods Hole Oceanography Institute and WH7805 from the Sargasso Sea (provided by B. J. Binder, University of Georgia, Athens, GA). Cultures were grown in the SN medium (44) at 25 °C in constant light ($\approx 25 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $1 \mu\text{E} = 1 \mu\text{mol}$) in an illuminated incubator. One liter of cyanobacterial culture collected at the late log phase was harvested by centrifugation ($10,000 \text{ min}^{-1}$ for 15 min). Cell pellets were resuspended with 1–2 mL of SN media, and kept at 4 °C until further analysis.

Purple nonsulfur bacteria are of interest for their capacity for anaerobic, nonoxygenic photosynthesis and growth with hydrogen production. We chose the versatile α -proteobacteria *R. rubrum* ATCC 11170 (G. P. Roberts, University of Wisconsin, Madison, WI) because they possess a well-characterized carotenoid light-harvesting apparatus, surrounding bacteriochlorophyll photocenters (22). In addition, the potential for a seminal role in the intracellular symbiosis mechanism during the formation of mitochondria by purple nonsulfur bacteria has been documented (25). The *R. rubrum* ATCC 11170 was grown in SMN medium (45) at 25 °C in 100-mL serum bottles

sparged with Argon and illuminated continuously with a 100-W desk lamp with rotary agitation at 2 min^{-1} . The *R. rubrum* was kept at its original culture.

The fresh maple leaf is of the variety *Acer rubrum* (red maple) picked from the NIST grounds August 21, 2007. Iron oxide control (Sigma–Aldrich; 12342–250G), a fine red powder that aggregates into a lumpy texture when placed in the Petri dishes (below), was used as a control.

Measurement Technique. Each sample was placed in a shallow Pyrex glass Petri dish, with depth and density adjusted by dilution with the culture medium to yield an absorbance close to unity in the absorption bands, measured using a spectrophotograph (Ocean Optics). The experiments were performed in 2 configurations, reflection and transmission, with minimal adjustment needed to switch between the two (Fig. 1). The small amount of polarization from the light source was measured without the sample in the beam and subtracted. Each sample was scanned in wavelength typically 3–5 times. Multiple measurements, typically 100, were obtained at each monochromator step of the full set of Stokes parameters simultaneously. All data at a given wavelength were combined to yield the mean polarization at that wavelength. Their dispersion was used to estimate the uncertainties on the mean. For some, a small amount of smoothing was applied in the wavelength direction and the uncertainty adjusted accordingly. Error bars show 1 SD from the resulting mean.

We derived the degree of linear polarization to check that the experiment is free of cross talk between the Stokes parameters. Scaled linear polarization curves are included in Figs. 2–4. Although linear polarization can change through absorption features, it does not mimic the circular polarization. The overall wavelength dependence is much flatter, and structure associated with the chlorophyll a sign change seen in circular polarization is absent in the linear polarization data. We believe the changes in linear polarization are due principally to changing light paths with optical depth, because the Petri dish base is not completely flat (slightly higher in the center). The Umov effect (46) whereby linear polarization is higher in regions of low albedo may also contribute to linear polarization features.

ACKNOWLEDGMENTS. We acknowledge support for this work through the Space Telescope and Science Institute Director's Discretionary Research Fund Grant 82374, and by the European Space Agency and National Aeronautics and Space Administration Grant NNX09AC68G (to S.D.).

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