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Dynamic Camouflage in Benthic and Pelagic Cephalopods: An Interdisciplinary Approach to Crypsis based on Color, Reflection, and Bioluminescence

Sönke Johnsen
Biology Department, Duke University
Durham, NC 27708
phone: (919) 660-7321 fax: (919) 660-7293 email: sjohnsen@duke.edu

Alison Sweeney
Physics and Astronomy Department, U. of Pennsylvania
Philadelphia, PA 19104
phone: (215) 573-7569 fax: (215) 898-2010 email: alisonsw@physics.upenn.edu

Daniel Morse
Marine Science Institute, U. of California at Santa Barbara
Santa Barbara, CA 93106
phone: (805) 893-8982 fax: (805) 893-7998 email: d_morse@lifesci.ucsb.edu

Dariusz Stramski
Marine Physical Lab, Scripps Inst. of Oceanography, UCSD
La Jolla, CA 92093
phone: (858) 534-3353 fax: (858) 534-7641 email: dstramski@ucsd.edu

Jules Jaffe
Marine Physical Lab, Scripps Inst. of Oceanography, UCSD
La Jolla, CA 92093
phone (858) 534-6101 fax: (858) 534-7641 email: jules@mpl.ucsd.edu

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http://www.biology.duke.edu/johnsenlab

LONG-TERM GOALS

Our overall goal is to understand the perceptual and mechanistic principles that underlay camouflage framed in the context of the animals' environment. In particular, we hope to characterize and understand the perceptual abilities of several species of benthic and pelagic cephalopods, the aspects of their optical environment that affect their camouflage behavior, the characterization of that behavior, and the molecular mechanisms inside the skin by which those responses are accomplished.

OBJECTIVES

1. To characterize the spatiotemporal characteristics of the near-surface and shallow benthic underwater light field, including ultraviolet radiation and polarization.

2. To determine the visual abilities of several species of cephalopod and model both the shallow and deep-water world from the animals' points of view.

3. To incorporate the knowledge gained from objectives 1 and 2 in order to study the camouflage behavior of these species under simulated ocean conditions.

4. To understand the underlying molecular and biophysical mechanisms governing changes in the skin that produce the observed optical effects, to provide a platform for future translational efforts.

APPROACH

Objective 1, Light measurements: Our approach to characterize the underwater light fields includes radiometric measurements with custom-built SQUID and Porcupine instruments and commercial hyperspectral sensors from TriOS(Germany) and Satlantic (Canada). SQUID (SeQuence of Underwater Irradiance Detectors) was developed for this project to provide a unique capability to measure both spatial and temporal statistical properties of downwelling irradiance fluctuations produced by surface-wave focusing within the surface ocean layer. The Porcupine instrument was developed for the ONR RaDyO program to measure temporal properties of high-frequency fluctuations in downwelling radiance and irradiance at several light wavelengths, and it complements SQUID measurements in this project. Both SQUID and Porcupine provide light measurements with a high sampling rate of 1 kHz. The TriOS and Satlantic sensors provide measurements of irradiance and radiance with an averaging time typically from about 0.002 to >1 s (depending on light intensity) and with high spectral resolution (~3 nm from 350 to 850 nm). Radiative transfer simulations are also used in this project as an additional tool to characterize the underwater light field.

Objective 2, visual physiology: our approach involves using microscopy, microspectrophotometry and the optomotor response to measure six primary visual parameters of the study species: field of view, spectral sensitivity, acuity, temporal resolution, and contrast and polarization sensitivity. Field of view is determined from the placement and orientation of the eyes and the geometry of the retina and pupil. Spectral sensitivity will be investigated using microspectrophotometry (MSP), which measures the absorption spectra of individual photoreceptors. Spatial and temporal resolution will be estimated from the spacing of photoreceptors in the retina and via the optomotor response. Contrast sensitivity is estimated by determining photon catch and also via optomotor assays using stripes of decreasing contrast. Polarization sensitivity will also be assayed via retina l morphology and optomotor response.

Objective 3, camouflage behavior: Camouflage behavior is studied both *in situ* and within various controlled environments, including a "holodeck", a tank surrounded by monitors that project natural environments or controlled visual stimuli. The top of the tank has a plexiglass "floatee" that will make the surface optically flat and permit undistorted observation of the animals from the outside as well as permitting images to be projected into the tank by two DLP projection systems.

Objective 4, biophotonics: We will characterize the optics of the skin using fiber-optic spectroscopy coupled with goniometry, measuring the polarization-specific bidirectional reflectance of the skin of

the target species and correlate these with the statistical analyses of the light measurements from objective 1 to determine which aspects of this complex reflectance have specifically evolved for camouflage. We will also determine the ultrastructure of the reflectin-based structures using transmission electron microscopy and model their optical effects to determine what aspects of the biological structures are important for the observed environmental optical match. We will also investigate the biophysical mechanisms governing tunable, self-assembling reflectance.

WORK COMPLETED

Objective 1, Light measurements and instrumentation development: The visual ecology of deep-sea animals has long been of scientific interest. In the open ocean, where there is no physical structure to hide within or behind, diverse strategies have evolved to solve the problem of camouflage from a potential predator. Simulations of specific predator-prey scenarios have yielded estimates of the range of possible appearances that an animal may exhibit. However, there is a limited amount of quantitative information available related to both animal appearance and the light field at mesopelagic depths (200 m to 1000 m). To mitigate this problem, novel optical instrumentation, taking advantage of recent technological advances, were developed by the Jaffe lab. In addition, during the reporting period the Stramski team has completed two major tasks: (i) analysis of power spectra of wave-induced light fluctuations at near-surface depths in the ocean under sunny conditions; (ii) a comprehensive suite of radiative transfer simulations of light field in the epipelagic zone of the ocean in support of the analysis of field data of horizontal spectral radiance collected on the KM12-10 cruise in the Pacific waters off Hawaii Islands. The results from the analysis of these field data are part of the collaborative paper led by Sönke Johnsen with participation of the Stramski team (Johnsen et al., in press). The analysis of results from radiative transfer simulations is underway. The paper on the characterization of light field within the mesopelagic zone was revised and published during the reporting period (Li et al., 2014) and we provided contributions to a collaborative paper on deep-sea light measurements (Haag et al., submitted). We also continued the analysis of field radiometric data which we collected during the project-sponsored cruises in the Gulf of California in 2010 and 2011. This analysis is focused on the effects of inelastic radiative processes and twilight conditions in the epipelagic layer of the ocean.

Objectives 2 and 3, visual physiology and camouflage behavior: We published a theoretical assessment of how perceptual mechanisms in most sensory modalities lead to specific predictions about the evolution of crypsis or conspicuousness. We also assessed signaling evolution in *Lolliguncula brevis* to determine what ecological factors cause them to break camouflage. To do this we analyzed videos of individuals signaling in different social contexts controlled in captivity. This manuscript is in prep. We also conducted trials to test whether *Metasepia pfefferi* produce a "passing cloud" display to confuse potential prey during attack. We are currently analyzing these data. In addition, we explored 'bioelectric crypsis'. We quantified behavioral and electrical responses of the cuttlefish to a video simulation of a looming predator (Fig. 1a). We then simulated the bioelectric fields of cuttlefish in a behavioral assay to quantify shark responses to these prey-simulating cues (Fig. 1b).

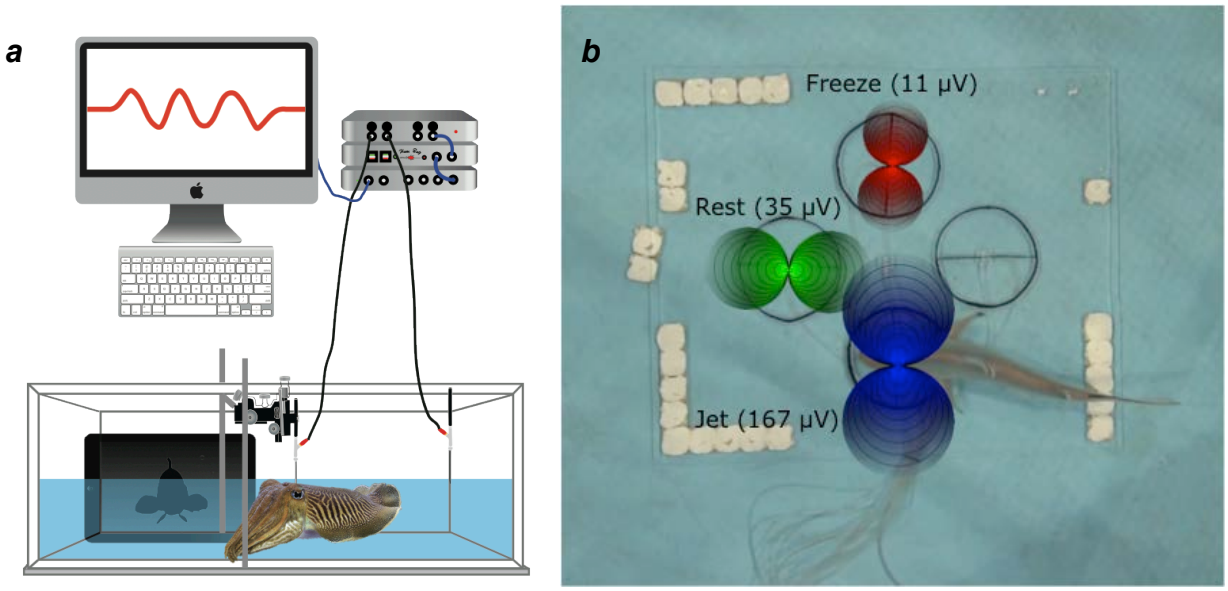

Figure 1. Experimental set-up for work completed in this study. (a) Electrophysiology and behavioral recordings from cuttlefish. A video of a looming fish predator was played on an iPad positioned along one wall of an experimental tank. Behavior (body movement from ventilation) and bioelectric field responses (associated with ion exchange during ventilation) were recorded over the course of the predator simulation with video cameras and a recording electrode positioned at the opening of the mantle. (b) Behavioral assay used in shark responsiveness experiments. Two species of shark were tested in a behavioral assay to determine if cuttlefish freeze-simulating electric fields decreased detection by predators relative to the rest and jet-simulating electric fields. A cuttlefish-simulating dipole electric field was activated via a pair of underwater electrodes at one of four locations (indicated by circles) on an acrylic array placed on the bottom of the shark experimental tank. Both stimulus (rest, freeze, or jet simulating) and dipole location (1-4) were randomly selected for each trial. Once a shark swam within the reference circle and passed the active dipole, the electrode pair was switched off. Each encounter (pass over) the circle was scored as "no response" or "response" and the percent responsiveness was compared using an ANCOVA with species as the covariate. Shark species were bonnethead sharks (*Sphyrna tiburo* n=7) and blacktip sharks (*Carcharhinus limbatus* n=9).

Objective 4, biophotonics: One of the real scientific surprises of this effort has been the vast array of photonic structural diversity to be found in the oceanic midwater – each new species we study seems to have a novel physical strategy for hiding in the void. This year we have characterized five novel photonic tissues that contribute to camouflage in midwater cephalopods and fish, including an interesting composite of Bragg-layered fibers responsible for directional counterillumination in *Galiteuthis*. We have also completed a bioinformatics analysis of the reflectins proteins responsible for the self-assembly of these tissues. In addition, we (1) identified "aquaporin" channels through which water is reversibly expelled and re-imbided to tune nanoscale dimensions of Bragg lamellae and Mie reflectors in two adaptive camouflage systems in squid skin, (2) discovered first clue to the role of reflectins' structure, and (3) identified molecular "hair-trigger" fine-tuning biophotonic control.

RESULTS

Objective 1, Light measurements and instrumentation development: As part of the Jaffe Lab work in this MURI, a portable optical imaging scatterometer was developed to measure angular reflectance, described by the bidirectional reflectance distribution function (BRDF), of biological specimens. The instrument allows for BRDF capture from samples of arbitrary size, over a significant fraction of the reflectance hemisphere. Multiple specimens representing two species of marine animals, collected at mesopelagic depths, were characterized using the scatterometer. Low-dimensional parametric models were developed to simplify use of the data sets, and to validate the BRDF method. Results from principal component analysis confirm that BRDF measurements can be used to study intra- and inter-species variability of mirrored marine animal appearance. Collaborative efforts utilizing the BRDF data sets to develop physically-based scattering models are also underway. Another key part of the deep-sea biological camouflage problem was examined via *in situ* measurement of underwater light fields. Here, two underwater radiometers, capable of low-light measurements, were developed to address the lack of available information related to the deep-sea light field. Quantitative comparison of spectral downward irradiance profiles at blue (470 nm) and green (560 nm) wavelengths, collected at Pacific and Atlantic field stations, provide insight into the presence of Raman (inelastic) scattering effects at mesopelagic depths. The radiometers were also used to measure bioluminescence.

Whereas the general pattern of depth dependence of wave-induced irradiance fluctuations was documented in a number of previous studies, there is very little published information for depths smaller than 1 m, and essentially no published data within the top 0.5 m of the ocean. In this report we present example results from unique measurements of wave-induced irradiance fluctuations within the top 1 m layer of the ocean, which were conducted by the Stramski team with the SQUID and Porcupine instruments during the Catalina Island experiment in 2011 (Gassmann et al., in prep). The maximum of power spectra of irradiance fluctuations at very small depths (0.1 - 0.5 m) under sunny conditions is observed within the frequency range of 2 - 4 Hz (Fig. 2). The magnitude of power spectra is very high at relatively weak winds between 3.5 and 5 m s^{-1}, which favor the strong wave focusing. Under very calm conditions with wind speeds < 2 m s^{-1} the magnitude of power spectra is significantly lower indicating a decrease in the intensity of irradiance fluctuations. Under favorable wind conditions the coefficient of variation of irradiance fluctuations at near-surface depths is as high as 0.8 and drops to values below 0.2 when the wind decreases to below 1 m s^{-1} (Fig. 3).

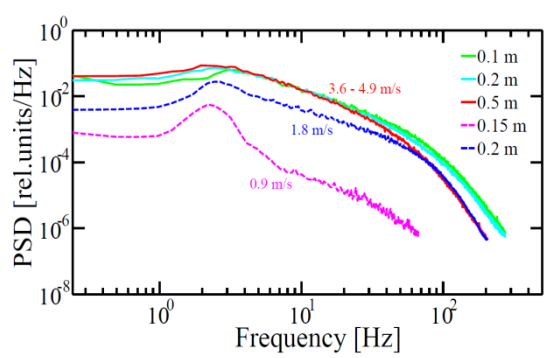

Figure 2: Power spectral density of fluctuations in downward irradiance measured within the top 0.5 m layer of water column at a light wavelength of 532 nm at different wind speeds as indicated. The measurements were made during the Catalina Island experiment on September 29, 2011.

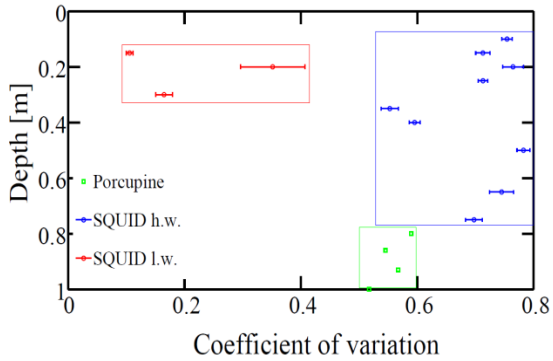

Figure 3: The coefficient of variation of fluctuations in downward irradiance measured within the top 1 m layer of water column at a light wavelength of 532 nm during the Catalina Island experiment on September 29, 2011. The measurements were taken with the SQUID and Porcupine instruments under two wind-wave regimes, i.e., relatively weak winds between about 3.5 and 6 m s^{-1} which favor strong wave focusing (blue and green data points) and very weak winds less than 2 m s^{-1} (red points).

Objectives 2 and 3, visual physiology and camouflage behavior : Our theoretical assessment predicts that in sensory modalities following Weber's law, animals trying to match a stimulus should err on the side of greater magnitude than the target stimulus. Animals trying to be conspicuous against a background should change towards lesser magnitude. Our study of signal function in *L. brevis* shows that females break camouflage more than males do, and signaling correlates with mating contact. Preliminary evidence suggests that females use signals to help males track them during a mobile courtship in a poor visibility turbid environment.

In addition, a group of experiments using the holodeck was performed in order to elicit, classify, and interpret cuttlefish responses to a various side and bottom visual stimuli. Processing of nearly 12,000 recorded responses by the animals yielded both interesting technical challenges in classifying the data and also in interpreting the variety of displays. Subsequent analysis by post-doctoral fellow Darcy Taniguchi indicated that the animals responses were more affected by the bottom panels, in contrast to the side ones. Although these initial efforts were accomplished by simple visual inspection and interpretation, a program to automate segmentation to extract the region of cuttlefish and automated classification was instituted. Here, students Justin Haag and Eric Orenstein were successful in creating algorithms to perform both automated extraction of the cuttlefish in the camera images as well as automated process of the images. The classification work processes the data set using a texton-based algorithm to codify traditional, manual methods of cuttlefish image analysis. In practice, the approach achieves an accuracy of ⇠ 94.2% as compared to manual annotation. An additional aspect of the analysis was the introduction and demonstration of a novel, data driven method for exploring the dimensionality of cuttlefish patterns.

Finally, we report a novel cryptic mechanism in the cuttlefish *S. officinalis* in which bioelectric cues are reduced via a freeze response to a predator stimulus (Fig. 4). The reduced bioelectric fields created by the freeze-simulating stimulus resulted in a decrease in predation risk by shark predators by reducing detectability (Fig. 5). The freeze response may also facilitate other non-visual cryptic mechanisms to lower predation risk from a wide range of predator types.

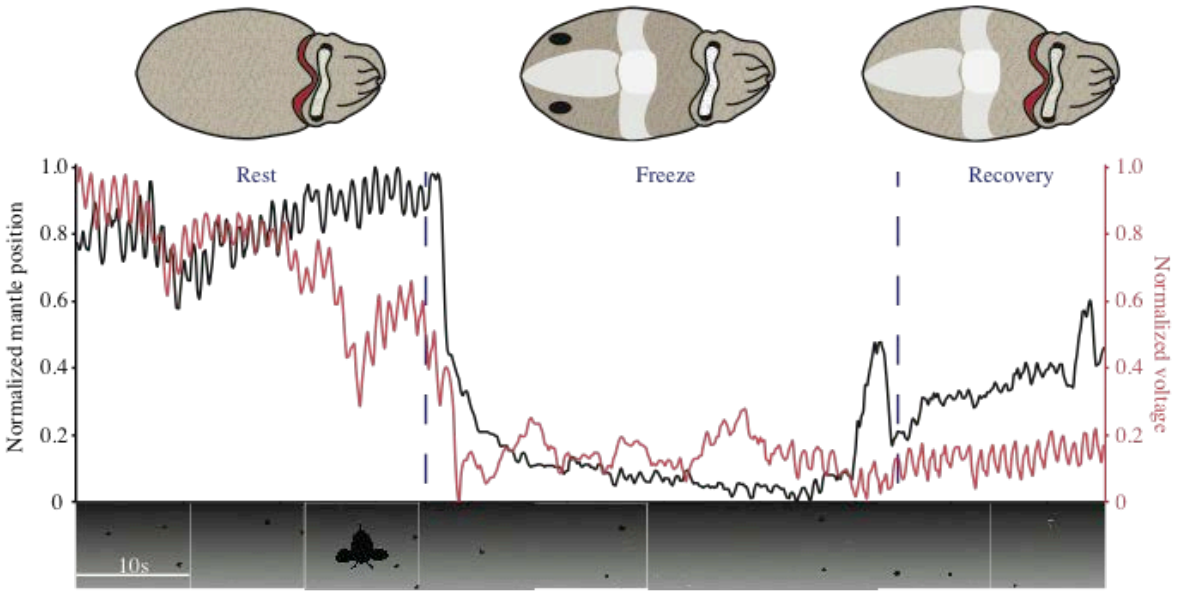

Figure 4. Representative response of Sepia officinalis to a video simulation of a looming predator. Both the frequency and amplitude of body movements and bioelectric cues were reduced by the freeze response. Amplitude data are normalized to the peak point in each trace for presentation purposes. Cuttlefish illustrations depict the typical camouflage and mantle cavity opening states for each phase of the recording. Rest = quiescent, resting animals. The gills were exposed laterally at the mantle cavity opening at the junction between the mantle and the head. Freeze = response characterized by motionlessness, flattening of the body, covering of the gills, and reductions in the amplitude and frequency of electrical cues. Recovery = transition from freeze response to the resting state. Camouflage and the amplitude and frequency of body movements and electric potential returned to within 1 SD of the resting state at the beginning of the recovery period. Resting mantle height and baseline voltage returned to within 1 SD of resting at the end of the recovery period (not shown). Black= body movement/motion, red= electric potential/voltage.

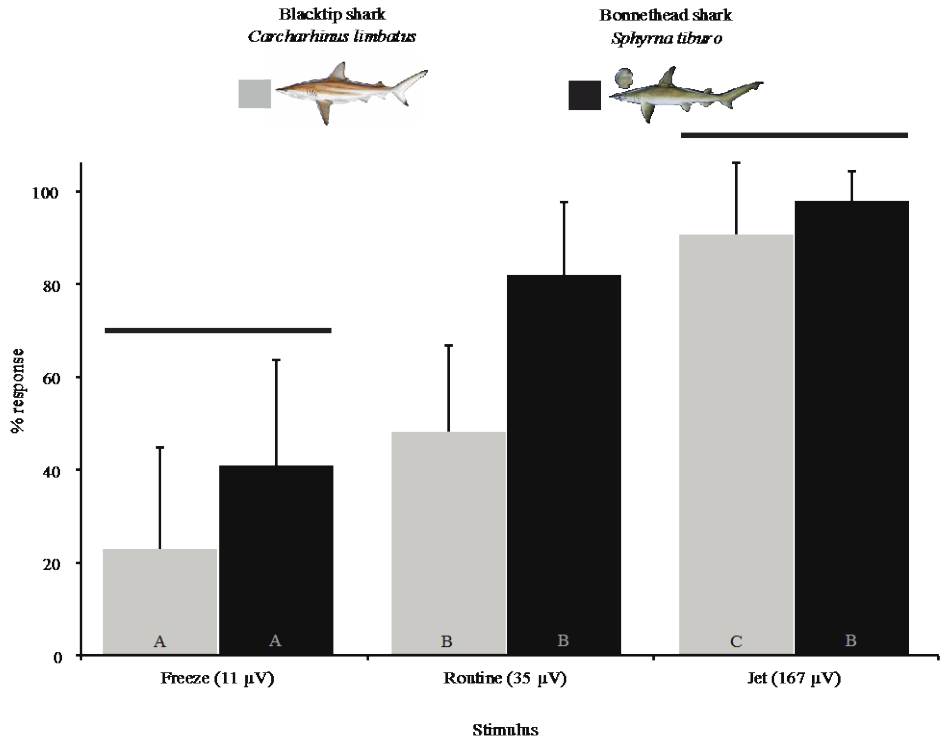

Figure 5. Shark detection of Sepia- simulating electric fields. Bonnethead sharks responded to freeze and jet-simulating electric stimuli significantly more frequently than blacktip sharks. Both species demonstrated the greatest proportion of responses to jet-simulating stimuli, with nearly 100% of encounters resulting in a bite response. Both species also demonstrated the fewest responses to the freeze-simulating stimuli. Bars represent the mean percent responsiveness ± SE. The lines connecting bars indicate no difference between species (α= 0.01). Bars for each species that share the same letter were not significantly different (α= 0.01).

Objective 4, biophotonics and instrumentation development : Our bioinformatics efforts have uncovered a real surprise in reflectins. They appear to be the most heavily RNA-edited tissue documented in any biological system to date. This finding has potential implications for our understanding of their function – a high degree of polydispersity is apparently important and under heavy evolutionary selection. Our finding of a novel light-guiding composite in *Galiteuthis* also has rich potential for inspiring novel materials. We have also used finite-difference time domain modeling to explain the highly structured, unusual BRDF result from the hatchetfish generated in the Jaffe effort.

The biophysical mechanism of reflectin-mediated biophotonic control that we elucidated is shown in this figure that accompanied a highlight of our discoveries from *The Scientist* (Fig. 6).

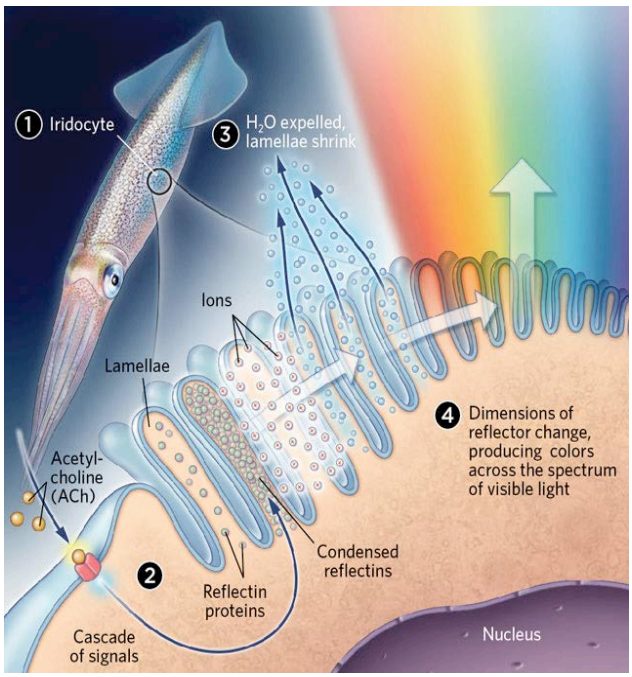

***Figure 6. A schematic illustrating the biophysical mechanism of reflectin-mediated biophotonic control (from* The Scientist).**

We now have characterized "aquaporin" channels in the Bragg lamellar membranes through which water is reversibly expelled and re-imbibed by Gibbs-Donnan equilibration in response to the reversible occlusion or exposure of charges on the surfaces of the reflectin proteins (governed in turn by the neurotransmitter-mediated activation of a signal transduction cascade controlling the site-specific phosphorylation of the reflectins, thereby tuning their reversible Coulombic repulsion or condensation). This reversible flux of water changes lamellar thickness and spacing to tune the reflected color. Location and function of aquaporin channels and their role in tunable biophotonic systems are illustrated schematically (Fig. 7).

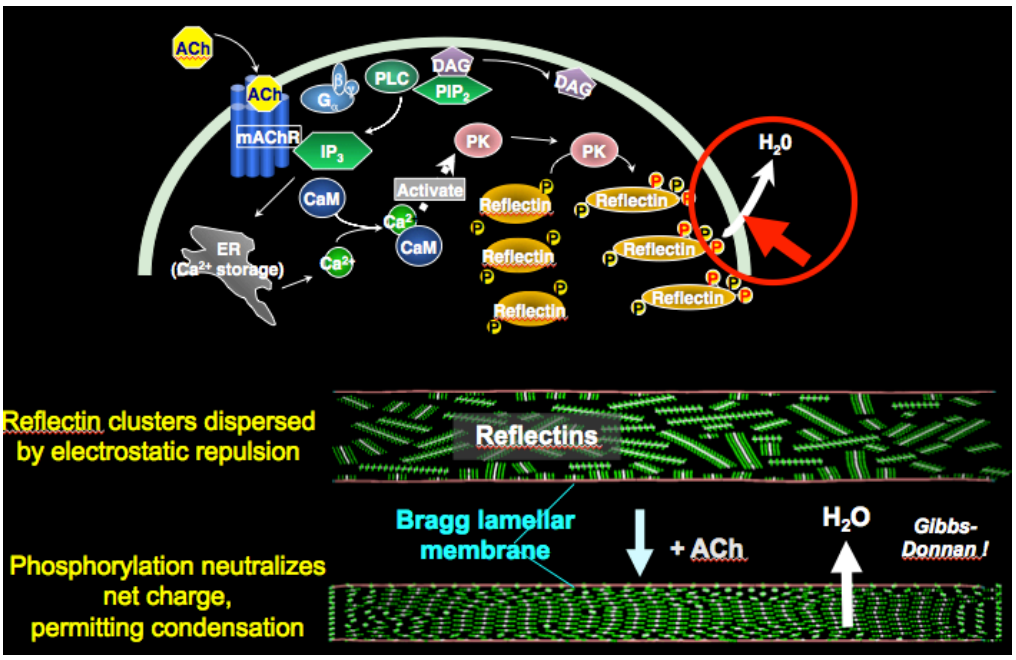

Figure 7. The location and function of aquaporin channels and their role in tunable biophotonic systems.

We have discovered the first clue to the role of the reflectins' structure, and learned that the reflectin-controlled molecular switch governing dynamically tunable camouflage in squids has a hair-trigger, with sensitivity further enhanced by the enzymatic upstream signal amplification pathway:

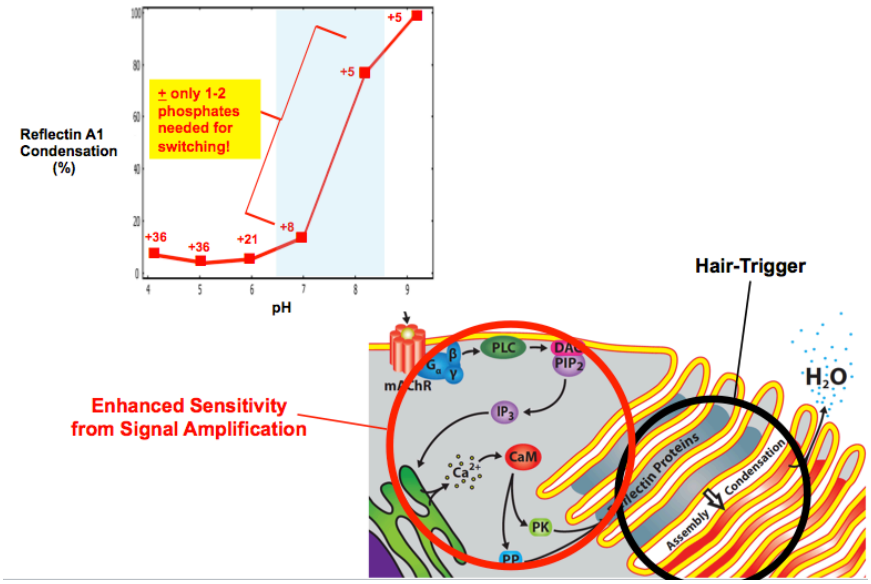

Figure 8. The effects of small differences in surface charge on condensation.

As illustrated above (Fig. 8), condensation of the reflectin proteins (ultimate trigger controlling the biophotonic response)is exquisitely sensitive to small differences in surface charge. Addition or removal of one or two phosphate groups can drive the reflectins over the full range of their reversible condensation or de-condensation. This "hair-trigger" sensitivity resides in the repeated sequence domains of the reflectins (previously a mystery). These domains reversibly form alpha-helices as the reflectins begin to condense, presenting amphiphilic structures with one "face" strongly hydrophobic, thus acting like a molecular Velcro to reversibly bind to other helices, driving the cooperative yet fully reversible condensation of the reflectins that in turn drives the Gibbs-Donnan dehydration and shrinkage of the Bragg lamellae. Sensitivity is further increased by the up-stream enzymatic (i.e., catalytic) signal amplifying signal transduction cascade.

IMPACT/APPLICATIONS

The systems evolved by marine animals in order to hunt, hide, and mate over hundreds of million years surpass our contemporary engineering designs for underwater vehicles. Hiding and hunting are natural tasks for our military and we believe that valuable clues will be provided by the results of our studies. The impact will hopefully affect all branches of the armed forces that have aquatic missions. This includes Special Forces, mine hunting vehicles, the submarine community, and a newest generation of underwater vehicles that could all benefit from the option of "stealth". Since visual methods play an important role in the mission profiles of all of these groups, the ability to enhance and hide from detection should be an important payoff.

The discoveries reported above point to simple new methods to achieve effective camouflage for moving objects and effective edge disruption in shallow-water and caustic day-time light environments. We have been working in close collaboration with partners at Raytheon Vision Systems Inc. since the start of this project, seeking to develop practical translations of the signature management and other useful technologies, materials and devices important to industry, the Navy and other units of DoD. Our focus is to develop low-power electrically switchable polymer-based materials for these purposes. Through this collaboration we have developed a prototype biologically inspired, lightweight, electrically switchable, polymer-based shutter for IR detectors that can be extended to coded apertures for IR imaging without a lens and to signature management in the IR (cf. patent awarded last year). In addition, the giant clam system may suggest novel geometries for devices for solar energy harvesting.

TRANSLATIONS

(1) <u>Electrically switchable, polymer-based shutters for IR detectors</u>: As described in our report, we discovered the molecular structures and mechanisms responsible for the dynamically tunable reflectance in skin cells of the squid, and are now working with Raytheon Vision Systems Inc. (with support from ARL and DARPA) to translate these finding to develop a prototype electrically switchable, polymer-based shutter for infrared detectors. Using solution-processable conjugated polymers, we developed working prototypes that are activated by low voltage (2-3 V) to display significant changes in absorption and reflection in the IR. As the polymer-based materials transition from semiconducting to conducting, free carriers and conformational changes absorb and scatter broad bands of infrared radiation. The resulting change in refractive index resulting from the simultaneous production of absorbing species and their increased density closely parallels the synergistic simultaneous changes in the reflectin-based Bragg layers that provide the high gain exhibited by the biological system. Defense applications include noiseless IR shutters for forward Special Forces

operations, graded neutral density and tunable hyperspectral IR filters, apertures, and lightweight coded apertures for IR image formation without a lens.

(**2**) **<u>Broadband, omnidirectional IR reflectors</u>:** Also as described above, we recently discovered that the silver, broadband reflective tissue surrounding the eyes of the squid (providing omnidirectional camouflage of that structure) is composed of a unique array of reflectin-filled, spindle-shaped cells densely packed together to form an unusual, quasi-disordered, "distributed Bragg reflector." The optical contrast between the high refractive index within these reflectin-packed cells and the low refractive index in the extracellular medium is responsible for the very high reflectivity of the tissue, while the infinite number of spacings between the nested, tapered cells in the quasi-disordered array is responsible for the broadband (i.e., multi-wavelength, silver) and omnidirectional reflection. Translating the underlying principles found in this biological broadband reflector (in research supported by ARO and Acumen, Inc.), we produced prototype broadband reflective coatings by evaporative self-assembly of asymmetric polymer rods to form quasi-disordered and "distributed" Bragg reflectors. The dimensions of the quasi-ordered polystyrene rods are sufficiently large to ensure that reflectance occurs in the IR, while the random quasi-disorder of the film ensures omnidirectionality of the reflectance. Silica and silicone casts of these organic films retain the optical properties in a rugged form suitable for device manufacture. Because the biologically inspired fabrication process is facile, error-tolerant and inexpensive and can be scaled to larger, flexible and curved surfaces; because silica and silicone casts preserve the desired optical features in a robust form suitable for manufacture of coatings; and because the optical and IR properties of those coating can be readily tuned, they offer numerous applications of potential importance to ONR and other branches of DoD.

RELATED PROJECTS

"Bioinspired Dynamically Tunable Polymer-Based Filters for Multi-Spectral Infrared Imaging"; DARPA; W911NF-08-1-0494; $150,000; 10-01/08-09/30/09. This work represents a "translation" of what we learned from the biomolecular mechanisms governing dynamically tunable reflectance in cephalopods to novel routes for synthetic optical materials. Performed in collaboration with Raytheon, Inc. This funding has ended; proposal for continuation is pending.

"Bio-inspired Visual Information Processing and Dynamically Tunable Multispectral IR Detection: Learning from the Octopus." ARL/ARO; W911NF-09-D-0001; $200,000; 1/1/09-12/31/09. To D.E. Morse and R. N. Hanlon. This work represents a "translation" of what we learned from the biomolecular mechanisms governing dynamically tunable reflectance in cephalopods to novel routes for synthetic optical materials. This funding has ended.

"Bio-Inspired Photonics: Polymer-Based, Dynamically Tunable Multi-Spectral Filters for IR Detection"; DARPA; proposal pending for continuation of effort described immediately above. This work represents a "translation" of what we learned from the biomolecular mechanisms governing dynamically tunable reflectance in cephalopods to novel routes for synthetic optical materials.

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