Optics of spider “sticky” orb webs

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1. REPORT DATE (DD-MM-YYYY) 06-10-2011
2. REPORT TYPE Conference Proceeding
3. DATES COVERED (From - To) -
4. TITLE AND SUBTITLE Optics of spider “sticky” orb webs
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6. PERFORMING ORGANIZATION NAMES AND ADDRESSES Macquarie University
   Biotechnology Research Institute
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   00000 -
7. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)
   U.S. Army Research Office
   P.O. Box 12211
   Research Triangle Park, NC 27709-2211
8. DISTRIBUTION AVAILABILITY STATEMENT
   Approved for public release; distribution is unlimited.
9. SUPPLEMENTARY NOTES
   The views, opinions and/or findings contained in this report are those of the author(s) and should not contrued as an official Department of the Army position, policy or decision, unless so designated by other documentation.
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Optics of spider “sticky” orb webs

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Keywords: spider web silk, spider web optics, refractive index, dispersion, birefringence, micro-optics, micro-lens, thin film.

1. INTRODUCTION

Individual spider species manufacture and spin up to seven different types of silk [1, 2]. The silk of which we are most aware in our daily lives is that used in spider webs. Much of the biological success of spiders can be traced to the evolution of successively more sophisticated and functional webs. The web as a mechanical device has been extensively studied. Research on the physics of spider silk has established that the mechanical properties of dragline silks include a unique combination of high strength and high elasticity [3]. The chemical characterisation of spider silk and ability to synthesise spider-dragline-silk-like proteins is well advanced [4-5]. The dragline silk of spiders, at least for individual species that have been studied, is attributed to being the strongest naturally occurring material. This strength has been the material property sought in synthesized materials inspired by biomimicry of spider silks [4-5]. It has also been appreciated that the biological function of the silks means that evolution has been the driver of complex material properties and silk structures that are a “best” compromise between competing requirements [6]. We propose that one of the key drivers for the evolution for new materials properties and device structures of silks used in orb webs, in particular, is to achieve favorable optical properties. Low visibility of the web in its ecosystem is the primary requirement, we suggest. But, many spiders also decorate their webs with silks that are highly visible to insect prey in order to attract that prey [7]. In these cases the composite web has an attractive element, perhaps a flower analog, apparently suspended in free space but in fact embedded in a low visibility capture mesh. Thus, we propose that many spider orb webs are sophisticated optical devices. Silks are known to be composed from a range of protein-based materials. A new insight is that these materials can be explored as bioinspiration for optical materials. The trade-offs in material properties and device structures of silks are even broader than has been appreciated to date. They encompass both the mechanical and the optical properties of the silks and webs. Optical properties may emerge as being as important as mechanical properties as a driver for evolution.

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Proc. of SPIE Vol. 7975 79750G-1
1.1 Orb webs & silks - structure & material

Visibility of spider webs has been studied in biology. Webs have been shown to have low visibility against a green background, consistent with the natural background when they are constructed in trees and shrubs [8]. An extensive study of the reflectance of silks from species representing several different spider families showed those from the family Araneidae have low UV reflectance [9]. The other optical phenomena of spider webs that has been scientifically studied is the color displays seen in orb webs under certain natural lighting conditions [10-13]. It is independent observation of these color displays that initiated our interest in the optics of spider webs. The biodiversity in spiders and their silks dictates that there may be many different ways in which optical properties, structure and function of silks and webs lead to favourable adaptations for spider survival. Here-in we restrict our discussion to genera from the family Araneidae which construct orb webs of highly transparent silks which have transparent adhesive droplets on their capture spirals. We call these sticky-orb-webs to differentiate them from cribellar-orb-webs. Webs constructed from cribellar silks achieve prey capture by entrapment within a micro- and nano-structured silk geometry and have no adhesive droplets.

Figure 1. Structure of a typical orb web (top, after [1]). The sticky spiral and the junctions between sticky spiral strands and radials are most relevant to the optics of the orb webs reported here-in. An example of an optical micrograph of a radial silk strand, a sticky capture spiral strand (with adhesive droplets) and a junction is also shown (bottom, reproduced from [29]). Magnification 20 ×, species of Argiope Keyserlingi (Saint Andrews Cross spider). These silk fibres are a few microns in diameter.
The color displays arising from such cribellar webs are structural color. In particular, we focus on the more highly evolved sticky-orb-web weaving genera from Araneidae such as araneus and argiope [14]. We hypothesise that low visibility and low UV reflection have evolved as highly sophisticated adaptations. A typical structure for these orb webs, along with an optical micrograph of a radial and a sticky capture spiral strand, and their junction, is shown in figure 1.

The radial and frame silks (also dragline silk) are spun from liquid silk protein produced and stored in the major ampullate gland of the spider. Dragline silk is differentiated from radial silk by the speed at which it is spun, which is typically 10 to 20 times faster than the spinning of radial silk. The silk is spun from multiple spigots on the abdomen of the spider and the radial silks are typically composed of multiple fibers within a single strand. The cross section of the individual fibers is close to circular. The diameter of radial threads is variable, both intraspecies and interspecies. Typical diameter values are: for Araneus eburneus 1-2 microns, and for Argiope keyserlingi 5-6 microns. These are both species that have been included in our studies. The bulk compositional structure of spun spider silk is believed to be well known and understood [15]. It consists of nanoscale protein crystals (β-sheets) in a matrix of amorphous protein (α – helices).

Spider silk is a semi-crystalline biopolymer which is almost exclusively protein with repeated sequences of the amino acids glycine and alanine [16]. The capture silk is spiraled onto the radial framework. The capture silk is a pair fibers spun from the flagelliform silk gland and coated with an aqueous, adhesive secretion from the aggregate gland. This aqueous secretion redistributes into a series of similar sized and spaced adhesive droplets along the capture silk, seeded by nodules of glycoprotein laid on the core fiber [17]. The secretion contains low-molecular-mass organic and inorganic compounds, a variety of small proteins, at least one high-molecular-mass phosphorylated glycoprotein, water, and likely some lipids [17].

1.2 Orb webs & silks – optical elements

Now that we have briefly introduced the form of the orb web we can identify the optical elements contained within it. The silk strands can be approximated as cylindrical, transparent fibers. The sticky droplets are approximately elliptical micro lenses, with the complication that they are threaded on a cylindrical fiber. The junctions between radial silks and the capture spiral are irregularly shaped masses of the transparent, aqueous secretion from the aggregate gland. Further, the study of the cross sections of radial/dragline silks by transmission electron microscopy shows the radial silks have an inner core of silk surrounded by up to 4 outer layers [18, 19] with thicknesses at the nanoscale. The capture silks are a cylindrical fiber with a thin film layer. The cross sectional structure of capture silks is as yet unknown, to our knowledge, but is likely to have nanoscale outer layers to the silk in common with the radial and dragline silks. Thus, the optical elements are micro-cylindrical scatterers, with the likelihood of thin film interference effects being prevalent due to both the aqueous layer on the capture silks and the nanostructured layers of the silk itself; and micro-lenses, both the symmetrical elliptical adhesive droplets on the capture silks and the irregular “lenses” of the junction adhesive.

1.3 Prior discussion of spider web color displays

Prior research on the color display of spider webs has been scarce. Greenler and Hable attributed the color displays of spider silks as being due to the peaks in the scattered light from the cylindrical silks occurring at different angles for different colors within the white light spectrum [11, 12]. The most current examination into the source of the colors observed in spider webs in sunlight, predating our own, have been done informally by Professor Zawischa at the Leibnitz University in Hanover [10]. He conjectures that the image of a spider silk an observer sees is due to the incident light being partly reflected at the surface of the silk; partly propagating through, and being refracted by, the silk; and partly being scattered/diffracted around the silk. Since the silk is so thin he suggests that the three effects cannot be separated. It is only under specific natural lighting and observation conditions that a single phenomenon can be more easily interpreted, he argues. From his observations in nature he attributes colors seen on the capture silks in transmission (sun behind the web) as being; sometimes due to the interference of light scattered by the array of sticky droplets on the capture spiral alone; sometimes due to light scattered from the axial sections in between the sticky droplets; and sometimes a combination. He has speculated that the display from the radial fibers could be similar to that observed from light scattering from rough or matt surfaces. Other displays he and many others have observed are droplets of dew on spider webs producing colorful rainbow patterns (commonly known as dew bows). These are readily interpreted as standard water droplet rainbows [20]. The dew drops are one to two orders of magnitude larger than the capture adhesive droplets. He has also indicated a similarity between the colors seen on capture silks in transmission and those observed in thin soap films. Thus, thin film interference may be some component of the observed colors. He notes an axial thread between the droplets can be shining brightly but will be affected by light scattered from the droplets. Another factor he
describes are the irregularities in the distribution and size of the adhesive droplets, producing small-scale color changes.

A summary of the observed effects and Professor Zawischa's hypothesis to their occurrence is listed in Table 1.

<table>
<thead>
<tr>
<th>Observed Optical Effect</th>
<th>Hypothesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Multiple droplets on capture spiral dispersing colors</td>
<td>Multiple beam interference</td>
</tr>
<tr>
<td>Radial threads illuminated</td>
<td>Light scattering from the rough surface of the silk thread</td>
</tr>
<tr>
<td>Droplets of dew on spider webs producing rainbow patterns</td>
<td>Dispersion of light from small dew drops to produce rainbows as do raindrops</td>
</tr>
<tr>
<td>Sequence of colors seen on capture spiral resemble those seen on soap films</td>
<td>Thin film interference – the silks are very thin</td>
</tr>
<tr>
<td>No colors observed when sun behind observer</td>
<td>Destructive interference due to different sizes of droplets</td>
</tr>
<tr>
<td>Colors change as a freshly constructed web ages</td>
<td>Adhesive droplets coalescing give different optical effects</td>
</tr>
</tbody>
</table>

1.4 Summary of what is to come

In the sections that follow we introduce observations and experiments that allow the testing of a number of hypotheses about the cause of the color displays in sticky-orb-webs. Section 2 reports observations in natural lighting and interprets these in terms of optics. These results show there are important optical elements which cause some of the color display types that have not been realized and proposed in earlier research. Section 3 reports light scattering studies which lead to the sound conclusion that light scattering plays little or no role in the color displays of sticky-orb-webs. Section 4 reviews other optical characterization experimental studies we have completed to measure the optical properties of silks and their associated adhesive coatings and droplets. Section 5 concludes on how these properties support spider silks and proteins emerging as a new biomaterial to be prospected for favorable optical properties and optical designs.

2. SPIDER ORB WEB COLOR DISPLAY IN NATURAL LIGHTING

Developments in digital photography support the collection of high quality digital images of the natural color displays of sticky-orb-webs, and indeed all webs. Due to length constraints we present one key example of this which leads to the new conclusion that the junctions of the sticky orb web are responsible for one of the dominant color display under certain conditions. Figure 2 shows a series of images of a sticky-orb-web suspended among trees. The images are taken from an orientation where the web is seen clearly against the dark background of a tree trunk. It is to be noted that this is a view from the side. The face-on views of this web are against a background of dappled light through leaves. The web has low visibility when viewed face-on, the intended approach direction for insect prey capture. The four images in figure 2 are taken with the same numerical aperture, and slightly different angles of view and camera-web distances. All the photos were taken within a ten minute time interval just before 9am on a late March morning (autumn in Sydney). The final image figure 2(d) has an exposure time three times that of the other images. The longer exposure leads to a brighter image but web movement within the exposure time increases the apparent footprint of the color display. This is shown more clearly in some of the enlargements that follow.

The images in figure 2 show a number of features which we have found to be common to all the studies of color displays we have completed. Firstly, for the light from the web to be registered by a camera or an eye it must be "specular" in nature. By this we mean it must be of small angular spread. If it is reflected from the web then it has derived from the backward scattering of a transparent cylindrical scatterer; and/or a strong specular reflection from a relatively flat faced junction; and/or a specular reflection, the white light of which has been dispersed due to propagation through a dispersive refractive medium. Given the finite numerical aperture of the camera or eye, when the specular light is also dispersed into an angular range, \( x \), say, it may be only a fraction of this angular range, \( ax \), where \( 0 < a < 1 \), that contributes to
Figure 2. Photos of a sticky orb web taken in late March (autumn) at ~9am in the morning, Sydney. All photos taken with a Canon EOS 400D digital camera using a 55 mm focal length lens with F number F/16. Exposure time 1/60 s in (a), (b) and (c); 1/20 s in (d). Angle of view of the web relative to the sun, and ambient lighting level vary between shots. The images show: I. in (a), (b), (c) & (d) – reflection and dispersion from junctions; II. in (b), (c) and (d) – forward scattering from radials colored via thin film interference. Photos Greg Staib.
the image, resulting in recording or seeing a color. For light to be seen following transmission by the web similar considerations apply. The angular range of the light must be constrained to be primarily “beam-like” if the light is to register strongly in vision or in a camera recording. The forward scattering by a transparent cylindrical scatterer of microns diameter is strong over a narrow range of angles around zero degrees. It will be white light unless modified by thin film interference or dispersion effects. This also implies a focusing or collimating phenomena is required by any refractive element in the path of the light if it is to result in a color display that can be imaged. In sticky orb web with four differentiated refractive and scattering elements: the junctions, the adhesive droplets, the liquid coated capture silks, and the radial silks; it will be the incoherent sum of the light propagating away from the web as a result of all the scattering, reflective and refractive paths resulting from the propagation of the white light that impinges on the footprint of the web that will constitute the light/color display of the web. This can range from the near invisibility of the web through a complex range of possible color displays.

We return now to discuss the specific displays seen in figure 2 in more detail. Enlargements of parts of each of these images are reproduced in figure 3. A further enlargement of a section of figure 3(c) and 3(d) is shown in figure 4. There are three distinct optical displays in the overall display. Firstly, all the images in figure 2 show bright spots arising from reflection and dispersion from the junctions. This is shown as display type I in the figure overlays. The junctions are approximately flat surfaced, irregularly shaped globules of the adhesive (set) (see figure 1). They have an approximately smooth optical surface which gives rise to a specular reflection of ~4% for normal incidence and higher for larger angles of incidence. White light can also be propagated through the volume of the junction globule, following a path determined by the laws of refraction and reflection, before reaching the eye or camera. In this case, depending on the angle of view, the dispersed light may appear separately from the specularly reflected white light and can be colored depending on the collection angle of the eye or camera and the distance between the “detector” and the web. We have shown in another study that the adhesive material is highly dispersive [21]. Note the globules are of a size (greater than 10 microns) where geometric optics remains an appropriate model for the micro-optics [22]. Display type II, is forward scattering from radials with coloring consistent with thin film interference. Note back scattering from radials can show similar effects but with much lower intensity. The layered structure of the radial silk is the likely candidate for the relevant thin film. A layer of order 50 -200 nm occurs for the few Araneidae silks that have been studied by TEM [18, 19]. The strongly reflected wavelength, λr, from a thin film can be calculated using eqn 1.

\[ \lambda_r = 2n_{silk}d_{film} \cos \theta_r / (m - 0.5) \]  

(1)

where

\[ \theta_r = \sin^{-1} \left( \frac{\sin \theta_i}{n_{film}} \right). \]  

(2)

θi is the angle of incidence onto the thin film; nfilm and ninner are the refractive indices of the thin film and the inner silk, respectively, dgel is the thickness of the thin film, θi is the angle of refraction in the film and m is the order of interference. The pastel colors are consistent with thin film interference and the repeating color sequence in the arcs of strong radial silk scattering: orange through pink to blue are consistent with calculations simulating the decreasing angle of incidence with a constant thin film thickness (in the range 0.1 -0.2 microns) due to the curvature in the web. A refractive index difference between the silk and film of 0.05 - 0.1 can give predictions consistent with the observations but there are no experimental measurements of this refractive index difference as far as we are aware. We are planning such measurements. A blue to orange transition will occur with a change in order of interference. The final display, type III, only becomes apparent in the enlargements. This is due to focusing and dispersion by the adhesive droplets on the capture silks. The detail of this is not fully resolved in the images, but 5x images show it clearly [21]. The footprint of these micro-lenses is smaller than the junction globules and therefore they collect less light. As well formed symmetrical elliptical lenses they are also better at dispersing the light in a rainbow sequence. However the variability of the droplet size means the rainbows from individual droplets do not reinforce each other in the way raindrop rainbows do [21]. In different lighting conditions this type III display can have higher intensity relative to the other displays discussed.

For both the type II and type III displays the full explanation of the optical propagation through droplets and junction globules needs to incorporate the internal silk(s) acting as scatterers within. The backscattered light from the internal silk can effectively act as an internal source. More complete research of this problem is planned.
Figure 3. These are enlargements of part of the respective images in figure 2. In the case of (a) the upper central section from fig 2(a) has been cropped and rotated right. For (b), (c) and (d) the section is from above and below and to the left of the hub of the web. The images show: I. in (a), (b), (c) & (d) — reflection and dispersion from junctions; II. In (b), (c) and (d) — forward scattering from radials colored via thin film interference; III. in (b), (c) and (d) — micro-lensing with dispersion from the adhesive droplets on the capture spiral.
Figure 4. These are enlargements of part of the images in figure 3(c) and 3(d) respectively. They show the colors arising from micro-lensing, with dispersion, from the adhesive droplets on the capture spiral. Figure 3(d) is out of focus due to the web movement in the air during the exposure. This shows the rainbow banding more diffusely than the specular quality of the image with better focus.

The images of a second sticky orb web are shown in figure 5. These show a color display which is dominated by type I - dispersion by the junction globules - optics. Here in the shorter exposure time, smaller numerical aperture image (b), and its cropped enlargement (c), a standard rainbow sequence of colours is shown with variation in angle of view. The web movement has streaked these "spots". Thin film interference within the main forward scattering lobe from some of the radials is also seen in (b) and (c). (a) shows that when the exposure is increased to an overexposure (which also simulates much higher lighting levels), and the numerical aperture is larger, the color displays are washed out by the much stronger white light forward scattering from the capture silks, the white light specular reflection and propagation by the junction globules and the collection of a larger angular range of dispersed light.
3. LASER LIGHT SCATTERING/PROPAGATION BY NATURAL SPIDER SILKS

It has been noted in section 2 that light scattering by highly transparent cylindrical spider silks shows a strong forward scattering lobe. This broadens as the diameter of the silk decreases. There is a trade-off here. As the diameter decreases the footprint of the silk in the path of the incident sunlight is reduced. Thus, the total light that will either be transmitted or reflected (the scattered light), or absorbed by the silk is reduced. But, the angular range into which it is scattered increases so that the insect prey has a greater probability of seeing (in UV) the forward scattered light from the axial silk sections, but at lower intensity. The light scattered from the capture droplets leads to further angular spread of the incident light. Using a standard code for calculating the scattered light distribution from a transparent cylinder gives the
results shown in figure 6. Here the light scattered by a 125 micron diameter silica fiber is contrasted with a 2 micron diameter spider silk. The ratio of back scattered light to forward scattered light for the optical fiber, parallel polarization, is ~ 1/1000th, whereas that for the 2 micron spider is ~ 1/110th. This larger ratio for the narrower cylinder explains why the silks can be seen in both "reflection" and "transmission". But no color display arises from this as all colors have a strong forward and backward scattered lobe which overlap to give a strong white light signal. This can be modified by thin film interference as is described in section 2.

![Graph](image)

Figure 6. Comparison of scattering by (a) a silica optical fiber (n = 1.456, λ = 633 nm) with diameter of 125 microns with (b) a spider silk (n = 1.538, λ = 633 nm) of diameter 2 microns. Light polarized parallel to the cylinder axis – blue trace, perpendicular polarization – red trace. The maximum intensity in the forward scattering is not plotted in (a). It is ~275 for the parallel polarization and ~220 for the perpendicular polarization. The values shown in (a) are not differentiated from the zero axis when the scattering intensity axis is scaled linearly to include the maximum scattered intensity. In contrast the backscattered light for the 2 micron silk has an intensity an order of magnitude smaller than the forward scattered light for parallel polarization, and is less than a twentieth for perpendicularly polarized light.

When considering the light scattered by the adhesive droplets on the capture spiral silks a laser light scattering experiment enables this to be shown. Figure 7 shows the layout of the experiment (left) and the scattered intensity distribution, scaled relative to the cylinder scattering which is the strong linear component through the center of the pattern in the central image. It is also contrasted with laser scattering of a radial shown in the right image. The angular spread of scattered light by a series of adhesive droplets on a silk (about 50 droplets are illuminated by the laser beam in figure 7) is large and ensures that this light component does not contribute strongly to color displays from the web. It diverges too rapidly with distance from the web for this to occur. As discussed in section 2 it is specular reflection type fields and beam-like transmission that result from refraction that can lead to the color displays from capture silks.
4. OTHER OPTICAL CHARACTERIZATION OF SPIDER SILKS AND WEB ELEMENTS

For the optics of spider webs to be able to be fully understood it is necessary for the optical material qualities and device specification to be quantified. Also, have accurate knowledge of the micro and nano-structure of the silk is needed. Optical refractive index, and its variation with wavelength, are key parameters. Silks have been measured as being birefringent [23-25]. The geometry and structural form of the adhesive droplets as micro-lenses is compound – the lenses are strung on the capture silks and the optical materials properties of all components needs to be known before the micro-lenses can be accurately modeled. The primary driver in evolutionary terms has been to achieve low visibility webs which also succeed as prey capture devices. The optical materials that have resulted, particularly the composite nanocrystallite/amorphous protein silks are a basically different optical material well worth further study for its biomimetic potential.

The refractive index of spider silks has been measured from laser scattering experiments assuming the silk is either a single, ideal cylindrical scatterer [12,13,23], or a double cylinder as is a more correct model of a capture silk [24]. The uncertainty in the measurements is large – between 2 and 20%. The Senarmont technique of polarization microscopy has been applied to the measurement of the birefringence of spider silks [25]. We have achieved a twenty times improvement in accuracy for the measurement of the refractive index dragline and radial silks using an image contrast immersion technique. Using this technique the refractive index of the silk can be calculated to within ±1 x 10^-4. The values within a web, and between webs spun by different spiders of the same species, are more variable than the measurement uncertainty. Values around 1.5500 have been measured for Araneus Eburnus with an Abbe number of ~32 and a birefringence up to 0.0133 [26]. This technique, and its variants being researched, will be applied routinely to measuring the refractive index of the silks of spiders. Once the refractive index is known the Fresnel reflection coefficients for a dielectric silk can be calculated. Techniques for measuring the absorption and nonlinear optical coefficients of the silks are being researched in our laboratory currently.

The optical quality of the finish on the silks and adhesive droplets is another feature of importance to the optical function of the web. Studies we have completed on radial silks by AFM [27], the capture silks and droplets by OSP [28], and the synthesis of the results from both these measures [29], show that the silks and droplets are optically smooth. This supports the conclusion that the color displays seen on sticky orb webs are not due to micro- or nano- structuring of the surfaces. It is still possible that such structural color is seen in webs using cribellar silk. The surface roughness of the silks of Argiope Keyserlingi were measured as less than 30 nm for radial and 5-6 nm for capture silks [28,29]. This is
optically "flat". Increasing this by a factor of 2 that takes account of possible sample flattening in the AFM procedure used [28] this corresponds to the capture silks having an effective optical smoothness of \( \lambda/50 \times (\lambda = 500-600 \text{ nm}) \). These values indicate the sticky orb web of *Argiope Keyserlingi* has optical finish. This is an outcome that is predicted to have arisen, with evolution as the driver, to achieve favorable optical function.

5. CONCLUSION

This research had a start point of wanting to understand the optics of the color displays of spider silks and sticky orb webs. Three specific color display types have been identified and interpreted here-in. They involve scattering by micron sized transparent cylinders combined with thin film interference, and combinations of refraction and reflection by tens of micron sized micro-lenses and junction globules. In making the measurements of the bulk optical properties of the silks that are needed to be able to model them meaningfully, it emerges that they are highly birefringent. This property most likely links to the composite nanocrystallite/amorphous structure of the inner core of the silks. It suggests the silks may have high nonlinear optical coefficients and are worthy of much further research to investigate their biomimetic potential. The spider silks and related materials emerge as interesting bio-optical materials to be prospected for optics – protein optics or proteo-optics.

ACKNOWLEDGEMENTS

The writing of this manuscript was supported by the U.S. Defense Advanced Research Projects Agency and the Army Research Office under contract number W911NF-10-1-0256. The authors thank Mr Adam Joyce for help with optical surface profiling, and Associate Professor Jim Rabeau, for supporting access to the AFM instrument. Both are with the Dept. of Physics and Astronomy at Macquarie University.

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