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Structural origin of the brown color of barbules in male peacock tail feathers

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We report detailed optical measurements and numerical simulations of brown barbules in male peacock tail feathers. Our results indicate that brown coloration is predominantly produced structurally by the two-dimensional (2D) photonic-crystal structure in the cortex layer of a barbule. The constructing strategies of brown coloration revealed by numerical simulations are indeed subtle, which are of great significance in the artificial constructions of mixed structural coloration. It is found that the structural configurations of the 2D photonic-crystal structure such as the lattice constant, the number of periods, and even the interdistance and missing holes between the two melanin layers nearest to the cortex surface, are important in the production of structural brown colors.

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Pigmentation is a primary way in color production. However, nature provides an alternative way—structural coloration [1–3]. Structural colors are produced by light interactions with microstructures with a featured size comparable to light wavelengths. Structural coloration in the biological world manifests significant functionality, such as signal communications, and even may convey important evolutionary information. Structural colors are quite widespread in the biological world, found in insects, moths, birds, and even in leaves [4–11].

In a recent study [12] we revealed that the diversified colors in male peacock tail feathers are produced by tiny two-dimensional (2D) photonic-crystal structures [13–16] in the cortex of barbules. Two interesting strategies to produce structural colors were found. One is to simply vary the lattice constant to cause diversified structural coloration, and the other is to enhance Fabry-Perot interference by the reduction of the number of periods in the 2D photonic-crystal structure in order to create an additional color, eventually giving rise to mixed coloration.

Structural violet, blue, green, and even yellow colors were found in the biological world. However, brown colors have been generally believed to be produced by pigments instead of by structures [17]. Brown colors are typical mixed coloration. If we could find strategies to produce structural brown colors, we would take advantage of these strategies to fabricate artificially nanostructures that can produce other mixed colors, opening a door for colorful applications.

In this paper, we show detailed experimental and theoretical evidence that the coloration of brown barbules in male peacock tail feathers is predominantly due to structures rather than pigments. The revealed means of constructing structural brown colors is rather interesting and indeed delicate, which are significant in the artificial constructions of mixed structural coloration.

Male peacock tail feathers were bought in a free market at Banna, Yunnan Province, China in 2001. The peacock tail feathers have a central stem with an array of barbs attached on each side. On each side of a barb there is an array of flat barbules. Each barbule has round indentations of typically 20–30 μm, which disperse natural light and cause coloration. It was found [12] that the transverse cross section of barbules is crescent. In general, barbules comprise a central medullary part, consisting of randomly dispersed keratin and melanin, enclosed by a cortex layer. Interestingly, the cortex layer contains a 2D photonic-crystal structure, composed of arrays of melanin rods connected by a keratin matrix with air holes. The lattice arrangement of the 2D photonic-crystal structure in blue, green, and yellow barbules is square, while in brown barbules it is rectangular. The schematic cortex structure of a brown barbule is shown in Fig. 1. The distinct structural differences among different colored barbules lie in the lattice constant and the number of periods (melanin layers) in the 2D photonic-crystal structure. The number of periods is about 10 in blue and green barbules and about 6 in yellow barbules. In brown barbules there is no air hole array between the two melanin layers nearest to the cortex surface. Moreover, the interdistance between two melanin layers nearest to the cortex surface is different from that between adjacent melanin layers in the 2D photonic-crystal structure. These two structural features are absent in blue, green, and yellow barbules. The number of periods in the 2D photonic-crystal structure in brown barbules is 4 or 5. For brown barbules, the lattice constant of the 2D photonic-crystal structure along the direction parallel to the cortex surface is $a_{\parallel} \sim 150$ nm, while that perpendicular to the cortex surface is $a_{\perp} \sim 185$ nm. The interdistance between the two melanin arrays nearest to the cortex surface is about 235 nm on average.

To explore the coloration origin of brown barbules, we measured the reflectance spectra of a brown barbule with and without glycerin infiltrated by a microspectrophotometer, shown in Fig. 2(a). This microspectrophotometer can probe a tiny area of a few square microns. The infiltration of other materials into air holes can alter the refractive index arrangement. If the positions of spectral peaks in reflectance spectra are altered after infiltration, one can ascertain that colors

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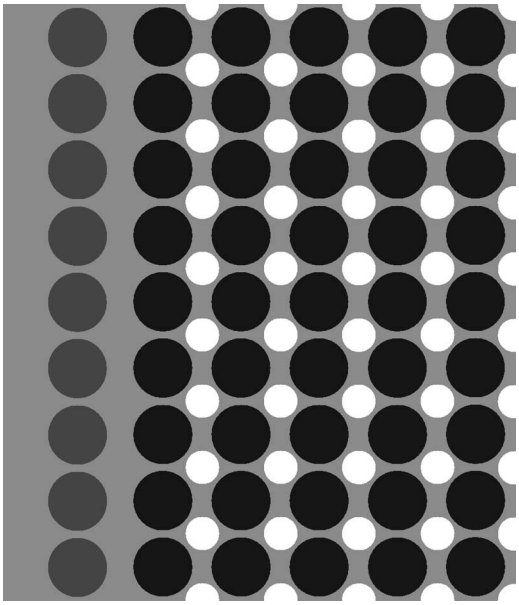

FIG. 1. Schematic microstructure (transverse cross section) of the cortex layer of brown barbules. Dark gray dots represent melanin rods nearest to the cortex surface. Black and white dots denote other melanin rods and air holes of the 2D photonic-crystal structure, respectively. Light gray stands for the keratin matrix. Note that one layer of air holes is missing between the two melanin layers nearest to the cortex surface.

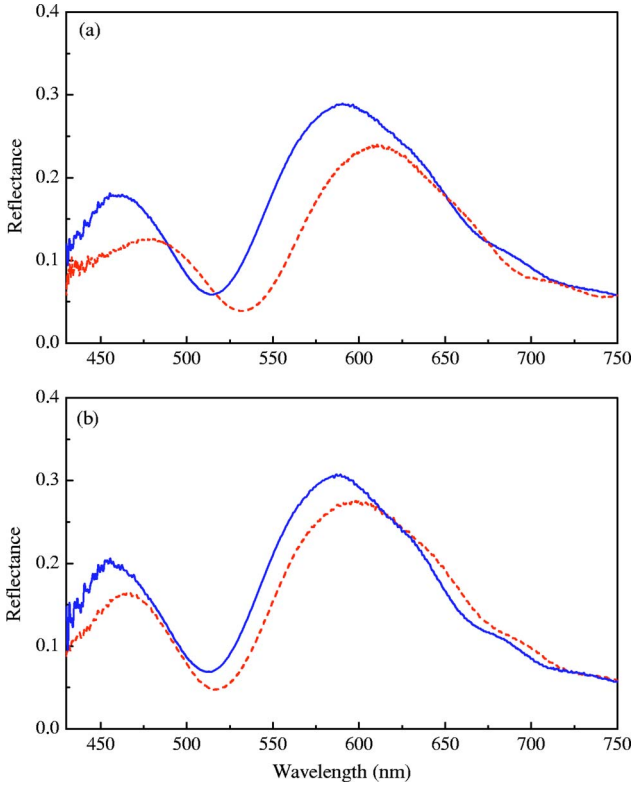

FIG. 2. (Color online) (a) Measured reflectance spectra of a brown barbule with (dashed line) and without (solid line) glycerin infiltrated for unpolarized incident light. (b) Measured reflectance spectra for incident light with E (solid line) and H (dashed line) polarizations.

should be mostly due to structural coloration. On the contrary, colors are due to pigmentation if the positions of spectral peaks are unaltered after infiltration. In the visible spectrum, two distinct spectral peaks can be resolved, one at blue wavelengths and the other one spanning from green, yellow, and orange to red wavelengths. These spectral peaks lead to brown coloration. Indeed, spectral peaks shift their positions to lower wavelengths after infiltration. The wavelength shifts are found to be rather small, about 20 nm, and hence do not change coloration very much. The evident shifts of the spectral peaks demonstrate unambiguously that coloration in brown barbules is predominantly produced structurally.

It is known that the optical properties of ordered photonic structures are generally polarization dependent. In 2D photonic crystals, E (with electric field parallel to melanin rods) and H (with electric field perpendicular to melanin rods) polarizations have different photonic band structures [15]. To study the polarization effects on coloration, we also measured the reflectance spectra for incident light with E or H polarization, shown in Fig. 2(b). The reflectance spectra of two polarization are similar, although there are some small differences in intensity and spectral peak position. Importantly, polarization does not influence coloration since the differences of the positions of spectral peaks for two polarizations are rather small, similar to other colored barbules [12].

Based on a converting method [11] we can convert a reflectance spectrum into RGB values for a given illuminant in order to study color changes. In this paper, we use the Commission Internationale de l'Éclairage (CIE) normalized illuminant D65, which closely matches that of the sky daylight. The converted RGB colors from the measured reflectance spectra show that the infiltration of glycerin does not alter coloration very much although there is a bit of brightness decrease. For different polarizations the situation is similar.

To get insight into how structural brown coloration is produced, we need to calculate the photonic band structures of the 2D photonic-crystal structure in the cortex layer, shown in Fig. 3 for both E and H polarizations. Photonic band structures are obtained by using a plane-wave expansion method to solved Maxwell's equations [15]. In photonic band-structure calculations, the structural parameters of the 2D photonic-crystal structure are taken from measurements. The radii of melanin rods and air holes are proximately taken to be $0.4a_{\perp}$ and $0.15a_{\perp}$, respectively. The refractive indices of keratin and melanin are taken to be 1.54 [6] and 2.0 [7], respectively. It is found that at low frequencies the photonic band structures for two polarizations are rather similar. The differences occur at high frequencies. No complete (along all directions) photonic band gap exists in this 2D photonic-crystal structure for both polarizations. However, there exist some partial photonic band gaps along certain directions. For example, there is a partial photonic band gap along ΓX (the direction normal to the cortex surface) for both polarizations. The midgap frequencies for both polarizations are similar, at about $0.28c/a_{\perp}$. This result is supportive to the experimental observation that polarization has a minor influence on coloration. There is also a partial band gap along $\Gamma X'$ (the di-

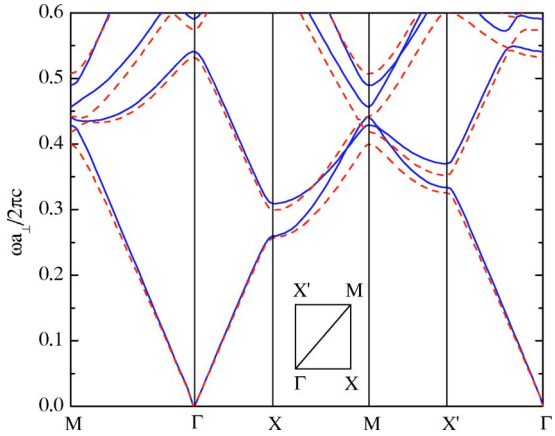

FIG. 3. (Color online) Calculated photonic band structures of an infinite 2D photonic-crystal structure of a rectangular lattice for E (solid lines) and H (dashed lines) polarizations. The inset shows the irreducible Brillouin zone. Note that the ΓX direction is along the direction normal to the cortex surface.

rection parallel to the cortex surface). This partial photonic band gap does not contribute to coloration since $\Gamma X'$ is parallel to the cortex surface. Other photonic partial band gaps lie at high frequencies which are out of the range of human perception. For example, the second partial band gap along ΓX is located around $0.56c/a_\perp$, corresponding to a wavelength of 330 nm, which is outside of the range of human perception. But birds may see this color since birds are tetrachromatic (they have an additional ultraviolet/violet receptor that mammals have lost). Along ΓX the midgap frequency of the partial photonic band gap is mainly determined by $a_\perp$ rather than $a_\parallel$. The photonic band structures of the 2D photonic-crystal structure in brown barbules are rather similar to those in blue, green, and yellow barbules although the lattice arrangement is rectangular in brown barbules and is square in blue, green, and yellow barbules.

As we knew, for light with frequency located into a complete or partial photonic band gap, strong reflection is expected. Thus the partial photonic band gap along the ΓX direction is responsible for the structural coloration in brown barbules. However, the partial photonic band gap for either E or H polarization ranges in wavelength from orange to red in the visible spectrum. To obtain brown colors, a blue component should be added. Thus, the partial photonic band gap alone cannot lead to brown colors and other mechanisms to produce a blue component should exist. As revealed by our recent study [12], Fabry-Perot interference between two surfaces of a material with finite thickness plays an important role in producing an additional color. The effects of Fabry-Perot interference should be largest in brown barbules since the number of periods of the 2D photonic-crystal structure in brown barbules is least. As shown below Fabry-Perot interference is just the mechanism to produce the needed blue component.

To show the role of Fabry-Perot interference on coloration, the reflectance spectra of a generic cortex structure with different number of periods in the 2D photonic-crystal structure shown in Fig. 1 are calculated by a transfer matrix method [18], shown in Fig. 4. The obtained reflectance spectra for both E and H polarizations are rather similar. Therefore, we only display the reflectance spectra of E polarization. The dominant spectral peak at orange and red wavelengths results from the partial photonic band gap along ΓX. Owing to Fabry-Perot interference there are oscillations of the reflectance spectra on both sides of the dominant peak, much more distinct at low wavelengths. The number of os-

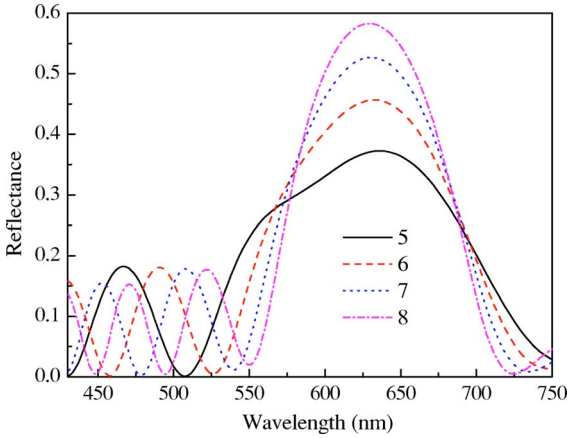

FIG. 4. (Color online) Calculated reflectance spectra of a generic cortex structure with different number of periods in the 2D photonic-crystal structure for E polarization.

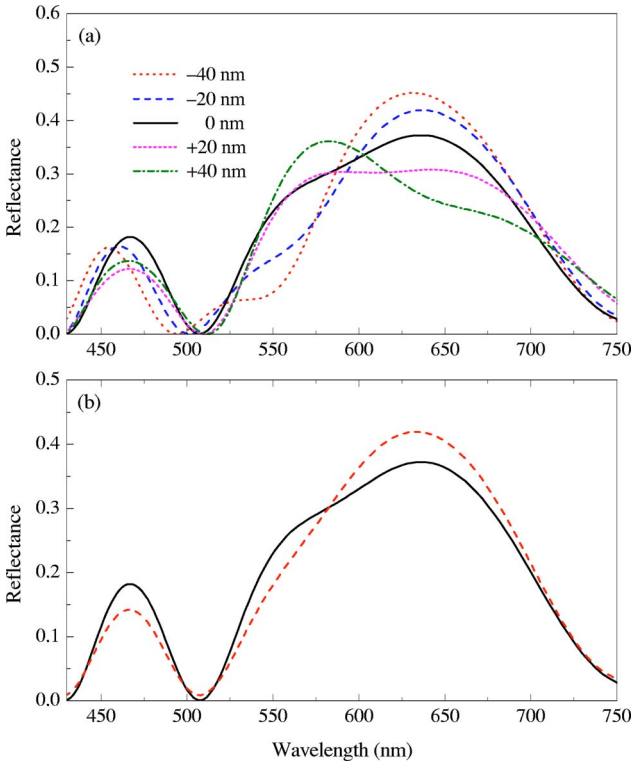

FIG. 5. (Color online) (a) Calculated reflectance spectra for different interdistance between two melanin layers nearest to the cortex surface for E polarization. The values in the legend indicate the relative change of the interdistance with respect to the real case. (b) Calculated reflectance spectra for two melanin layers nearest to the cortex surface with (dashed line) and without (solid line) air holes for E polarization.

cillations increases with increasing number of periods. The calculated reflectance spectrum for the structure with five periods in the 2D photonic-crystal structure (mostly close to the real situation) captures the main features of experimental results although there are some differences. This is not surprising since the real structures are far from ideal as assumed in our simulations. With increasing the number of periods from 5, the intensity of the dominant peak due to the partial photonic band gap increases, while on the lower wavelength side of the dominant peak, more oscillations due to Fabry-Perot interference appear. The intensities of these oscillatory peaks slightly decrease with increasing number of periods. Resultingly, the oscillatory peaks give minor contributions to coloration for large periods since they are rather small compared to the dominant peak. However, with decreasing number of periods, the oscillatory peak does give a contribution to coloration, leading to a mixed color eventually. The converted RGB color from the calculated reflectance spectrum for the structure with five periods agrees well with that converted from the measured one. With increasing number of periods, coloration has more orange and red components, making color turn orangelike or reddish.

As aforementioned, in brown barbules the interdistance between the two melanin layers nearest to the cortex surface is different from that between two adjacent melanin layers in the 2D photonic-crystal structure. Besides, there is no air hole array between the two melanin layers nearest to the cortex surface. These two features are rather important in producing structural brown coloration, as can be seen from Fig. 5. With decreasing interdistance between the two melanin layers nearest to the cortex surface from the real case, the orange and red components increase, while the blue peak exhibits a blueshift together with a decrease in intensity, making coloration turn orangelike or reddish. When increasing the interdistance, the orange and red components decrease, the yellow and green components increase, and the blue peak becomes a bit smaller. The changes of color components as a whole can counteract each other, leading to just a slight change in coloration, which is confirmed by the converted RGB colors from the calculated reflectance spectra. The missing air holes between the two melanin layers nearest to the cortex surface is also significant in producing brown coloration. If an array of air holes is introduced, there appears an increase in the orange and red components and a decrease in the blue component, turning coloration reddish.

In conclusion, we studied experimentally and theoretically the optical properties of brown barbules in male peacock tail feathers. We found that brown colors are predominantly produced by structural coloration. The constructing strategies of structural brown coloration revealed are very subtle. The lattice constant, the number of periods, and even the interdistance and missing holes between the two melanin layers nearest to the cortex surface are important in the production of structural brown colors. The revealed constructing strategies could be of great help not only in understanding physical mechanisms of structural brown coloration but also in fabricating artificial nanostructures that can produce mixed structural coloration, leading to potential colorful applications.

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