

Behavioral evidence for cone-based ultraviolet vision in divergent bat species and implications for its evolution

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ABSTRACT. We investigated the reactions of four bat species from four different lineages to UV light: *Hipposideros armiger* (Hodgson, 1835) and *Scotophilus kuhlii* Leach, 1821, which use constant frequency (CF) or frequency modulation (FM) echolocation, respectively; and *Rousettus leschenaultii* (Desmarest, 1820) and *Cynopterus sphinx* (Vahl, 1797), cave and tree-roosting Old World fruit bats, respectively. Following acclimation and training involving aversive stimuli when exposed to UV light, individuals of *S. kuhlii* and *C. sphinx* exposed to such stimuli displayed conditioned reflexes such as body crouching, wing retracting, horizontal crawling, flying and/or vocalization, whereas individuals of *H. armiger* and *R. leschenaultii*, in most cue-testing sessions, remained still on receiving the stimuli. Our behavioral study provides direct evidence for the diversity of cone-based UV vision in the order Chiroptera and further supports our earlier postulate that, due to possible sensory tradeoffs and roosting ecology, defects in the short wavelength opsin genes have resulted in loss of UV vision in CF bats, but not in FM bats. In addition, Old World fruit bats roosting in caves have lost UV vision, but those roosting in trees have not. Bats are thus the third mammalian taxon to retain ancestral cone-based UV sensitivity in some species.

KEY WORDS. Chiroptera; evolution; fear conditioning; UV vision.

Vision is fundamentally important in the animal kingdom, for example in mate choice, communication, and foraging. Mammalian retinæ have rod photoreceptors for night vision and cone photoreceptors for daylight and color vision. For color discrimination, most mammals possess two cone types with spectrally different visual pigments (opsins) that have absorption maxima at short wavelengths (Ss, blue or ultraviolet light) and middle/long wavelengths (M/Ls, green or red light). Although bats are the second largest order of mammals, the role of vision in their lives has seldom been considered because most have small eyes and it has long been hypothesized that an evolutionary “tradeoff” has occurred between their poor vision and their unique hearing ability associated with echolocation (SPEAKMAN 2001, ZHAO *et al.* 2009). Many studies have however investigated bats’ visual orientation and acuity in the past decade (EKLOF *et al.* 2002, RYDELL & EKLOF 2003, HOLLAND *et al.* 2005). Behavioral experiments in dark-adapted conditions have revealed that a phyllostomid, *Glossophaga soricina* (Pallas, 1766), can detect UV light (WINTER *et al.* 2003) and has stimulated related research.

Sensitivity to UV light is achieved by photoreceptors in the eye that contain a class of visual cone pigments maximally sensitive to light at wavelengths <400 nm (HUNT *et al.* 2001). WANG *et al.* (2004) studied the M/L and S cone opsin genes from

three bat species and suggested that the S opsin gene controlling sensitivity to UV light should retain its function. Our lab sequenced those opsin genes in 33 species with diverse sensory ecologies and found that the S opsin gene of bats had undergone a dramatic divergence among four lineages (ZHAO *et al.* 2009). Among the Yangochiroptera and Rhinolophoidea, gene defects in high-duty-cycle echolocators using constant frequencies (CF bats) should result in loss of UV vision, but not in those using low-duty-cycles (frequency modulated or FM bats). Among Old World fruit bats (Yinpterochiroptera) roosting in caves with low-ambient light, UV vision should be lost, but not in tree-roosting species. Based on the coevolved theory of vision and hearing of bats (SPEAKMAN 2001, ZHAO *et al.* 2009), the possible evolutionary sensory tradeoffs between shortwave vision and echolocation and changes in roosting ecology are consistent with the results of examination of S opsin among 28 species of bats from these four lineages using immunohistochemistry (MULLER & PEICHL 2005, 2006, MULLER *et al.* 2007, KIM *et al.* 2008, FELLER *et al.* 2009), though the exact spectral tuning of S opsin cannot be directly established. Recently, MULLER *et al.* (2009) employed corneal electroretinograms (ERGs) to corroborate the postulated UV spectral functions of the S opsin genes physiologically in the phyllostomids *G. soricina* and *Carollia perspicillata* (Linnaeus, 1758). However, we still cannot directly include bats among the

mammalian taxa that retain ancestral cone-based UV vision, because ERGs merely detect the capacity of photoreceptors for perceiving UV light, and they may have a function unrelated to vision, such as circadian rhythm regulation (NEI *et al.* 1997) and/or endocrine modulation (BRAINARD *et al.* 1994). Previous studies have only inferred that bats have the prerequisites for cone-based UV vision (MULLER *et al.* 2007, 2009) and no study has tested this capacity in the order Chiroptera. The search for UV vision in mammals has so far focused mainly on specialized cone types. WINTER *et al.* (2003) suggested that the possible rod-modulation (beta-band) mechanism for UV light perception in the bats' eye was still unknown while for other mammals it remained a possibility.

Because their retinas typically contain only a relatively small population of cones (ca 3% in bats with laryngeal echolocation, even less than 0.5% in Old World fruit bats, MULLER & PEICHL 2005, 2006, MULLER *et al.* 2007, KIM *et al.* 2008), it is difficult to study the nature of cone-based vision in nocturnal mammals (JACOBS *et al.* 2001). Following methods used for the demonstration of possible cone-based pathways (JACOBS *et al.* 1991, AMIR & ROBINSON 1996, JACOBS *et al.* 2001, ARRESE *et al.* 2006, PALACIOS *et al.* 2010), only behavioral studies can confirm proposed UV vision (JACOBS 1993, GRIEBEL & PEICHL 2003). Classical fear conditioning occurs when an affectively neutral stimulus (conditioned stimulus – CS) is paired with a noxious aversive stimulus (unconditioned stimulus – US) such as footshock (WALKER *et al.* 2002). This method could enlarge the neutral stimulus and has been successfully used in numerous species (from snails to humans, SANGHA *et al.* 2003, KINDT *et al.* 2009). Here we modified fear conditioning procedures to elucidate the bats' capacity for cone-based UV vision, since it is now well established that bats have functional visual systems and the corresponding anatomical evidence shows that both their cornea and lens can transmit UV light (MULLER *et al.* 2007, 2009). Our experiment was carried out under light conditions to avoid possible rod interference. Based on our molecular data mentioned above, the aim of the present investigation is to test our hypotheses that CF bats such as *Hipposideros armiger* (Hodgson, 1835) (Hipposideridae) and cave-roosting Old World fruit bats such as *Rousettus leschenaultii* (Desmarest, 1820) (Pteropodidae) have lost UV vision, and no longer react to UV light stimuli, but FM bats such as *Scotophilus kuhlii* Leach, 1821 (Vespertilionidae) and tree-roosting Old World fruit bats such as *Cynopterus sphinx* (Vahl, 1797) (Pteropodidae) have retained UV vision. The results will also indicate the diversity of cone-based UV vision in the order Chiroptera and provide further insight into the evolutionary history of visual capacities of diverse bat species.

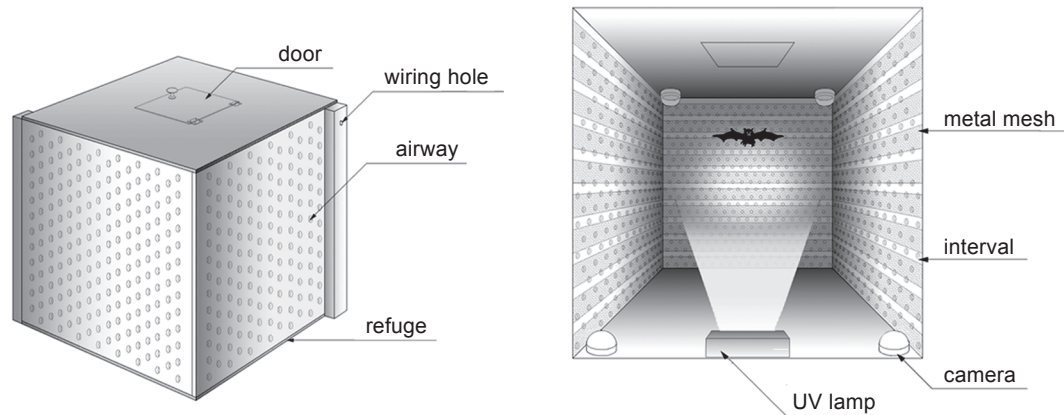
MATERIAL AND METHODS

Adult *S. kuhlii*, *R. leschenaultii* and *C. sphinx* were captured in Hainan Province, China, and *H. armiger* was captured in Yulong Cave, Anhui Province, China. The bats of each spe-

cies were housed together in an individual mesh cage (80 × 80 × 80 cm) in a ventilated temperature-controlled (24°C) feeding room (5 × 6 × 3 m). In the daytime (12:12 h light/dark cycle), the transmitting light provided by two fluorescent lamps (18W, Philips, Guangdong, China) was around 100 lx (measured with a calibrated luxmeter, Shenzhen Sampo Instrument Co., Shenzhen, China) in the inner cages. With *ad libitum* access to fresh water and weekly vitamin supplements, the two bat species with laryngeal echolocation were offered mealworms and two Old World fruit bat species were offered apples and/or bananas. The experiments were conducted at least three weeks after the animals were captured to ensure that they had acclimated to their new environment. In this study, the use of animals was approved by the Animal Experimental Ethical Committee of East China Normal University and followed its ethical guidelines for the care and use of animals.

Six bats of each species were tested. The experiment was operated in a ventilated wooden chamber (1 × 1 × 1 m) (Figs 1 and 2), the ceiling of which contained a square door hinged on one side. The floor insulation provided a temporary refuge for the bats especially when we were selecting and adjusting stimulus time and intensities during the training phases. The internal sidewalls were covered with twelve 5 cm-wide horizontal copper net bands with a three cm interval between them, from which the animals could cling and complete electrical circuits during the training and cue-testing. The metal bands were wired to a hand-operated shock scrambler and generator. Ultraviolet light was provided by a 6W UV hand lamp (365 nm, 20 nm half bandwidth, Spectroline, NY, USA), the radiant energy 15 cm away from which was 900 μm/cm². Before experiments, the lamp was placed on the floor of the chamber. Four infrared cameras inside the chamber were placed diagonal to one other, two on the roof and two on the floor so that almost all of the chamber could be monitored. A computer that ran Super-DVR software (DVR4Net PCI card) and interfaced with the cameras recorded events inside the chamber in real time. The wooden chamber was placed in the feeding room, adjacent to the bats' cages. The door was opened and together with the ventilation holes in the sidewalls provided persistent light illumination of around 100 lx during daytime experimental procedures. The bats thus experienced similar environmental conditions during behavioral experiments and possible interference from other environmental cues except UV light (CS) was reduced.

Behavioral procedures consisted of an acclimation phase, a training (fear-conditioning) phase, and a cue-testing (extinction) phase. In the acclimation phase, bats were introduced individually into the chamber for approximately 30 minutes per day for a week prior to the training phase to reduce the stress associated with handling and acquainting them to the chamber, which they explored by crawling and/or resting on the metal bands. Each day animals were handled at different times of day (09.00-16.00 h) to ensure that they did not entrain to handling by the experimenter at a specific time.



Figures 1-2. Schematic drawing of the chamber: (1) showing the profile of the chamber from the outer view; (2) showing the internal layout. The structure and components of the chamber are labeled.

On the day of training, bats were placed individually into the chamber and the experiments did not begin until the bats showed no obvious activity. Then the UV lamp was placed opposite to the bat. Each bat received 10 CS-US trials. A 0.4 mA, 1 sec shock was delivered after a 3 sec UV light stimulus (around 25 μm^2 , measured with a power meter, Phycience Opto-Electronics Co., Beijing). The stimulus parameters used in the experiment strictly complied with the detailed behavioral protocols for examining the nature and properties of fear extinction in laboratory rodents (CHANG *et al.* 2009), as bats are comparable in size to mice or rats. As soon as they suffered from footshock, each individual vocalized and flew, showing acute responses. The average inter-trial interval was three minutes (range, 2-5 min). During these intervals, we frequently adjusted the positions of the lamps with respect to the bats to ensure that the eyes of bats could perceive the UV light. FANSELOW (1980) pointed out that the distinct CRs observed immediately after shocks were similar to those after a delay of 24 hours. So in this phase, we gradually established the criteria for CRs in the bats (CS, 3 sec; 3 min inter-trial interval), as this was the first time that fear conditioning had been attempted in the order Chiroptera. For *S. kuhlii* and *C. sphinx*, the training procedures were carried out and persisted for about one week until distinct CRs were observed and stabilized. Conditioned reflexes were quantified by reflexes such as body crouching, wing retracting, horizontal crawling and/or vocalization, and flying as soon as the bats received the CSs. However, for *H. armiger* and *R. leschenaultii*, after two weeks training, we were still unable to observe distinct CRs. Since fear conditioning is a form of one-trial learning (FANSELOW 1990), here we could assume a robust and long-lasting behavioral change had been produced after these days of training among all individuals of four species.

For cue-testing, animals were returned individually to the same conditioning chamber. Followed the training procedures, each individual was continually exposed to a total of 100 UV

light CSs (3 sec; 3 min inter-trial interval) in the following two or three days. However, due to the repeated presentation of CS in the absence of the US, the conditioning response would be reduced (fear extinction, CHANG *et al.* 2009). During this process, each 10 CSs ended with one CS-US trial to strengthen the effect of conditioning and the behaviors of each individual, whether reflex or not when they received UV light only under light conditions, were recorded. Lastly, we calculated the conditioned reflex rates for each species by averaging the positive activities (CRs) per 100 CSs among six individuals and due to limited independent samples for each species, we also applied Mann-Whitney U-tests for pairwise comparisons between species.

RESULTS

During the training phase, each individual of all four bat species experiencing CS-US trials showed the distinct acute reflexes of vocalizations and flying. But in most of the sessions, *H. armiger* and *R. leschenaultii* did not show obvious CRs in the absence of US. As soon as they received UV light, the bats kept still, merely shaking their wings slightly or occasionally crawling along the metal-net bands. They also crouched and sometimes even flew, especially during the first two or three training days. Therefore, we temporarily categorized them as the group testing negative while the other two species, *S. kuhlii* and *C. sphinx* tested positive because they clearly showed fear and had distinct CRs once UV light was delivered: body crouching, wing retracting, horizontal crawling and/or vocalization and flying. In one to two weeks of training, we assumed CRs of all individuals were strengthened and stabilized and arrived at the optimal stimulus parameters.

In the cue-testing phase, we observed a total of 100 UV light CSs for each individual. The maximum value for conditioned reflex rates for individual *H. armiger* and *R. leschenaultii* (testing negative) was 20 – far less than the lowest ($n = 91$)

achieved for *S. kuhlii* and *C. sphinx* (testing positive). The average conditioned reflex rates and the statistical pairwise comparisons among the four species are shown in Fig. 3: the two testing groups were clearly different (e.g. *H. armiger* vs *S. kuhlii*, $U = 0$, $p < 0.01$; *R. leschenaultii* vs *C. sphinx*, $U = 0$, $p < 0.01$) while within groups there was no difference (e.g. *H. armiger* vs *R. leschenaultii*, $U = 9$, $p > 0.05$; *S. kuhlii* vs *C. sphinx*, $U = 8.5$, $p > 0.05$).

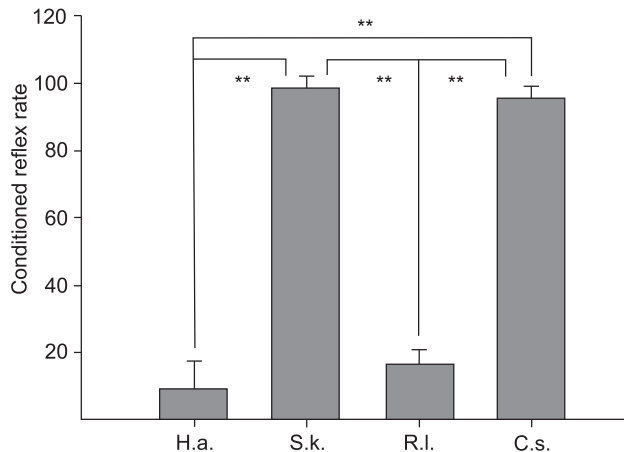


Figure 3. Histograms of the conditioned reflex rates for four species of bats (values = mean + standard deviation, Mann-Whitney U-test). H.a.: *H. armiger*, S.k.: *S. kuhlii*, R.l.: *R. leschenaultii*, C.s.: *C. sphinx*. ** $p < 0.01$.

DISCUSSION

Our behavioral study in four species among four lineages of bats found clear differences in the reactions of divergent bat species to UV light stimuli and provides direct evidence to suggest the diversity of cone-based UV vision in the order Chiroptera. It also supports previous molecular postulates from our own and other laboratories (WANG *et al.* 2004, MULLER & PEICHL 2005, 2006, MULLER *et al.* 2007, KIM *et al.* 2008, FELLER *et al.* 2009, ZHAO *et al.* 2009).

Among bats with laryngeal echolocation, *H. armiger*, as a member of the Hipposideridae-Rhinolophidae CF lineage, has lost the capacity for cone-based UV vision (no obvious CRs) but can utilize Doppler shifts, the most advanced nocturnal sensory adaptation within mammals, to receive and process a more continuous flow of acoustic information (HIRYU *et al.* 2005, JONES 2005). In contrast, *S. kuhlii*, belonging to the FM group, including all members of the Yangochiroptera and independently the Yinpterochiropteran taxon *Megaderma spasma* (Linnaeus, 1758) (JONES & TEELING 2006), has retained UV vision (evident CRs), which presumably can be used for orientation and/or hunting. Our previous work presented evidence of

independent losses of shortwave opsin functionality early in the evolution of the Hipposideridae-Rhinolophidae lineage according to the phylogenetic and molecular evolutionary analyses of S opsin genes in bats, indicating a possible evolutionary sensory tradeoff between vision and hearing in these two lineages (ZHAO *et al.* 2009). Combined with our current work, it seems that CF bats, with the evolution of a novel form of echolocation, may have rendered dichromatic color vision redundant and lost it, whereas FM echolocators can augment their acoustic “image” with UV vision. In Old World fruit bat lineages, the cave-roosting *R. leschenaultii* has lost cone-based UV vision (no obvious CRs) while the tree-roosting *C. sphinx* has retained it (evident CRs). This indicates that loss of UV vision may be correlated with roosting ecology, i.e., different levels of ambient light. Tree-roosting species at exposed daytime roosts appear to require UV vision to aid their visual discrimination for predator surveillance (MULLER *et al.* 2007) while cave-roosting species may not require color discrimination and experience a relaxation in selective constraint of the S opsin gene, ultimately resulting in loss of UV vision (ZHAO *et al.* 2009).

Following consecutive acclimation and training, we made UV light the unique cue to produce the obvious CRs in *S. kuhlii* and *C. sphinx* under light conditions. This differed from the approach of WINTER *et al.* (2003) who gave bats a non-illuminated stimulus in dark-adapted conditions. They reported a possible rod-modulation mechanism, because at that time, due to technical limitations, bats, as the group of mammals best adapted to the nocturnal aerial feeding niche, were still mostly considered to lack cones. In view of bats’ low light tolerance (HOPE & BHATNAGAR 1979, FURE 2006), any chromatic adaptation they adopted might render the intensity of stimulus provided too weak to show that they possess a separate UV light receptor as do rodents (JACOBS *et al.* 1991, JACOBS & DEEGAN 1994). In addition, we can rule out the possible interference of rods and avoid the corresponding contradiction between the photoreceptor data indicating cone monochromacy and the behavioral data indicating some capacity for color vision, as in whales and seals (GRIEBEL & PEICHL 2003). Because the secondary absorption peaks of “cis” from rods are more sensitive than those in cones to short wavelengths (GOURAS 1984), under mesopic lighting conditions, residual color vision in these cone monochromats could be achieved by exploiting the signal differences between the remaining green cones (L/M cones) and the rods. However, our experiment occurred in the daytime and rods could be bleached under such bright light conditions (PEPPERBERG 2003). Other than possible contextual interference (CHANG *et al.* 2009), *H. armiger* and *R. leschenaultii* exhibited no more reflexes during most cue-testing sessions although they had rod photoreceptors but lacked functional S cone photoreceptors. Meanwhile, the recent finding that cones were never blinded by light (LOBANOVA *et al.* 2010), might rationalize our procedures and the bleaching effect could not interrupt the cone-based visual pathway in bats, i.e. if *H. armiger* and *R. leschenaultii* possess functional S cones, they should

also exhibit distinct CRs, as did *S. kuhlii* and *C. sphinx* under the same light conditions.

Until now the exact rod-based (beta-band) mechanism for UV vision in mammals has not previously been demonstrated (WINTER *et al.* 2003). However, recent electrophysiological investigations revealed that the rods of bats could perceive partial UV light with cones under low mesopic light conditions (0.03 lx, MULLER *et al.* 2009). Therefore, to judge whether there are two mechanisms acting simultaneously to modulate UV vision of bats, further research is required.

In conclusion, our work widens our understanding of the evolution of cone-based visual capacities in the Chiroptera and the fact that some species retain cone-based UV vision means that bats are the third mammalian taxon to do so (JACOBS *et al.* 1991, JACOBS *et al.* 2001, ARRESE *et al.* 2006, PALACIOS *et al.* 2010). To further our work, corresponding field investigations are now also required.

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