RESEARCH ARTICLE

Arctic reindeer extend their visual range into the ultraviolet

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Accepted 18 February 2011

INTRODUCTION

The visual system of most mammals spans a spectral range of approximately 400–700 nm (Kelber et al., 2003; Bowmaker, 2008). Arctic mammals such as reindeer (Rangifer) experience extreme photic conditions with long periods of permanent light in summer and darkness in winter. In addition, polar regions have proportionally high levels of environmental UV light because of a high degree of atmosphere (Rayleigh) scatter and reflections from snow and ice (Weatherhead et al., 2007). Thus, diffuse radiation becomes the dominant element in the global radiation pattern in the blue–violet part of the spectrum, contributing to the characteristic blue colouration of the Arctic twilight environment, in mid-day in midwinter and during dusk and dawn in spring and autumn.

If significant amounts of UV light enter the reindeer eye, it is possible that the retina uses this information, although it carries the risk of retinal damage. One reason for thinking that UV vision might be of use to this Arctic mammal is that objects that absorb UV would have high contrast against the highly reflective snow surface. In light of this it is interesting to note that lichens (e.g. Cladinae) that form a key part of the reindeer winter diet do not reflect UV light (Petzold and Godward, 1988).

The aim of this study was to determine the sensitivity of Arctic reindeer to this part of the spectrum. We therefore measured the spectral transmission through their cornea and lens at a range of wavelengths down into the UV. We also recorded the electrophysiological responses from their retina to such stimulation. The results showed that UV light was transmitted through the anterior eye and that the retina responded electrophysiologically to this transmission. We also performed a molecular genetic analysis to determine the type of receptors that are responsible for the UV response.

MATERIALS AND METHODS

Animals

Male Arctic reindeer [Rangifer tarandus tarandus (Linnaeus 1758)] 15–20 months old were used in this study. They were purchased from semi-domesticated herds belonging to Sámi pastoralists in Troms and Finnmark counties, Norway (69–70°N). Experiments were conducted at the University of Tromso (69°46′N) where the animals had ad libitum access to concentrate feed and water or snow. They moved freely in large outdoor pens subjected to natural photoperiod and ambient temperature. Experiments were performed in June and December and, because there were no significant differences in results generated at these two time points, the data have been pooled. All electrophysiology experiments took place between 09:00 and 18:00 h. Each trial lasted 3–4 h, including the dark adaptation time, and was limited in duration and therefore in the number of interventions by how long we could keep each animal safely anaesthetised. After completion of experiments, animals were killed by bleeding following a blow to the head using a retractable bolt pistol. Permission to conduct experiments on reindeer was granted by the National Animal Research Authority of Norway.

Measurements of lens and corneal spectral transmission

One eye was removed from five separate animals immediately following death and the cornea and lens were dissected and frozen at −20°C. Subsequently, they were thawed and individually mounted in air and scanned in front of an integrating sphere using a Shimadzu
The cornea and lens transmitted near UV, with the wavelength of 50% transmission at 322 and 385 nm, respectively (Fig. 1). There was little variation in the transmission characteristics between individual animals. Hence, near UV passes into the reindeer eye.

Electrophysiological recordings from the retina
To determine whether the reindeer retina detects UV and, if so, by what mechanism, ERG responses to UV, blue, green and white stimuli from threshold were recorded. The LEDs chosen were selected with the aim of differentiating between rods (human rod $\lambda_{\text{max}}$=498 nm) (Dowling, 1987; Brown and Wald, 1963) and short-wavelength cones (human short-wavelength cones $\lambda_{\text{max}}$=420 nm) (Brown and Wald, 1963; Bowmaker, 2008). Although the LED matches for these were not perfect, the stimulus was designed with a view to examine the spectral balance of the retina. The experiment was limited by commercial availability and/or cost and the need to use an LED-based system because of portability. ERGs were established for white light (420–620 nm) as a reference.

Fig. 1. Spectral transmission profiles for reindeer cornea (black, N=5) and lens (red, N=5). The dotted lines represent ±1 s.d. Both structures transmitted down into the UV to approximately 300–320 nm. The difference between the corneal and lens transmission, with the cornea transmitting more light at nearly all points including UV, is due to its relative thinness in relation to the lens.
The first physiological response detected by the retina at low intensities is the STR, which is the main negative deflection seen in Fig. 2 (column 1). As intensity is increased, a small positive wave appears on the leading edge of the STR; this is the developing b-wave (arrow, upper row, Fig. 2). This increases in prominence and reduces in time to peak until the STR (Fig. 2, column 2) is obliterated by the b-wave (Fig. 2, column 3). The overall response profiles to each of the stimuli were similar. At the low energy levels used to establish threshold, it is usually only the rods that should respond without cone input (Rushton and Powell, 1972; Norby et al., 1984). However, as the green stimulus used was close to the maximum sensitivity of rods, it should elicit a greater response for a given stimulus intensity than that found to blue stimuli at similar low energy levels, but this was not the case. Hence, it is possible that both rod and cone photoreceptors are responding at very low light levels in the UV–blue range.

Human rods and cones have different temporal response characteristics (Hecht and Shlaer, 1936; Kelly, 1974; Hogg et al., 2007). To determine whether UV was detected by rod and/or cone photoreceptors, the temporal characteristics of the UV response at low luminance levels (1.8 μW) were investigated (Fig. 3). These showed no change in b-wave amplitude between 1 and 5 Hz. Beyond 5 Hz there was a steady reduction in b-wave amplitude with increasing stimulus frequency. Human rods do not respond above 18 Hz, but the short wavelength sensitive cones responded up to 25 Hz (Hogg et al., 2007); therefore, it is likely that there is a cone input at these low luminance levels, which at lower frequencies is masked by the rod input. Hence, the UV stimulus is rod mediated at low luminance levels, but short wavelength cones appear to also respond to this stimulus even though it is below their normal threshold (Auerbach and Wald, 1955).

**Molecular genetics: cloning and sequencing of the SWS1 opsin gene and spectral analysis of the encoded pigment**

A full-length coding sequence for reindeer SWS1 opsin, which encodes the pigment present in short-wavelength cones, was
obtained by PCR amplification using retinal cDNA as a template and primers designed to the sequence of bovine SWS1 opsin. Phylogenetic analysis (Fig. 4) confirmed the identity of this sequence as the reindeer SWS1 orthologue (GenBank accession no. FN808318). The sequence encodes Tyr at site 86 (Cowing et al., 2002; Fasick et al., 2002), which indicates that it will generate a violet-sensitive rather than a UV-sensitive pigment. UV pigments have Phe at site 86. In vitro expression (Carvalho et al., 2006; Cottrill et al., 2009) confirmed the absence of a specific UV-absorbing pigment; the resulting pigment, when regenerated with 11-cis-retinal, gave a peak spectral wavelength of the green stimulus (525 nm) is comparable with that of human short-wavelength cones at 435 nm. (Cowing et al., 2002) and somewhat long-shifted compared with Old World primates at 430 nm.

DISCUSSION

These results reveal that near UV enters the Arctic reindeer eye and that their retinae respond to this electrophysiologically. Genetic analysis reveals that sensitivity to such short wavelengths is not mediated by a separate UV receptor. At low levels it is rod mediated and at higher levels it is probably mediated by short-wavelength cones.

There are two main photoreceptor types in the retina, rods and cones, with the former mediating achromatic vision at low luminance levels and the latter mediating chromatic vision at higher luminance levels. The peak spectral wavelength of the blue stimulus used here (450 nm) is comparable with that of human short-wavelength cones (420 nm) (Brown and Wald, 1963; Dowling, 1987; Bowmaker, 2008). The peak spectral wavelength of the green stimulus (525 nm) is comparable with the peak sensitivity of human rods (498 nm) (Brown and Wald, 1963; Dowling, 1987). LEDs with more specific tuning frequencies were not available at the time of experimentation. Experiments to determine the energy levels required to generate scotopic responses showed similar responses to blue, UV and green stimuli. However, as the level of illumination was in the scotopic range, much smaller energy levels should have been required for the green as this favours rods.

Rods and cones have different temporal characteristics. Human rods do not respond to frequencies above 18 Hz (Hecht and Shlager, 1936; Kelly, 1974) and short-wavelength-sensitive cones do not respond to frequencies above 25 Hz (Hogg et al., 2007), but long/medium-wavelength-sensitive cones respond to frequencies exceeding 60 Hz (Hecht and Shlager, 1936; Kelly, 1974). Here, a 1.8 μW UV stimulus was temporally modulated, and the electrophysiological results suggest that this stimulated rod photoreceptors at these low luminance levels. Had this energy level been in white rather than UV light, it would have been firmly in the lower human rod range. However, it is important to stress that these are human data and not for UV light. As light levels increase and there is a switch to cone function, the role is probably taken over by short-wavelength cones as responses were found up to 25 Hz, which is the response limit of human cones and beyond that of human rods. However, again it is important to stress that these comparisons are between species and white light and UV (Hecht and Shlager, 1936; Kelly, 1974; Hogg et al., 2007).

Ideally, these experiments would have been extended to include those that generated comprehensive spectral sensitivity functions and measurements of chromatic adaptation. However, the experimenters were limited by the local availability of equipment, the ad hoc nature of the experimental conditions and the length of time deemed safe to keep reindeer anaesthetised. It is known that some rodents (mice and rats), bats and marsupials respond to UV stimulation (Calderone and Jacobs, 1995; Deeb et al., 2003; Winter et al., 2003; Hunt et al., 2009). However, the mechanisms responsible for UV vision and the potential function of this ability are likely to be different between reindeer and rodents for two reasons. First, rats and mice are nocturnal and photophobic, hence their UV exposure is likely to be minimal. Second, mice have
There are two obvious potential advantages for reindeer extending their visual range into the UV. First, one key food item, lichens of the genus Cladonia, displays strong absorption in the UV relative to its absorption in other visible wavelengths (Petzold and Goward, 1988). Furthermore, it has also been shown that wolf and white fur generally exhibits low UV reflectance (Reynold and Lavigne, 1981; Lavigne and Oristland, 1974). Thus, for the reindeer, both their preferred feed and their main predators appear with enhanced contrast against general UV-reflecting backgrounds. An additional potential benefit of UV sensitivity may be related to the fact that the UV reflectance of snow changes with the quality of its surface (Meinander et al., 2008), which could be of importance for the reindeer both in foraging and local movement on what may otherwise appear to be a bland surface.

Exposure to UV can produce a photokeratitis known as snow blindness where the cornea suffers a form of sunburn (Hemmingsen and Douglas, 1970; Collier and Zigmam, 1987). There is no evidence for snow blindness in Arctic mammals, and the explanation for this is unknown. The presence of scavenging components such as ascorbic acid (Ringvold, 1980) and seasonal changes in the cornea (Ringvold et al., 2003) have been suggested as ameliorating factors. That the anterior eye of this animal is permissive to UV also raises the question of why this radiation does not damage the neural retina. In relation to this, it is interesting to note that no Arctic mammal appears to display photophobia or attempt to avoid light exposure, behaviours that are typically found in UV-sensitive rodents.

ACKNOWLEDGEMENTS

This research was supported by the British Biotechnological and Biological Sciences Research Council. We thank Livia dos Santos Carvalho for helpful discussions.

REFERENCES


UV vision in reindeer  2019


