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INFLUENCE OF NEAR-ULTRAVIOLET RADIATION ON REPRODUCTIVE AND IMMUNOLOGICAL DEVELOPMENT IN JUVENILE MALE SIBERIAN HAMSTERS

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Summary

The aim of this study was to characterize the lenticular ultraviolet transmission of the Siberian hamster (*Phodopus sungorus*) and to probe the range of near-ultraviolet (UV-A, 315–400 nm) and visible wavelengths (400–760 nm) for modulating the photoperiodic regulation of its reproductive and immune systems. Ocular lenses from adult hamsters were found to transmit UV-A wavelengths at similar levels to visible wavelengths, with a short-wavelength cut-off of 300 nm. Five separate studies compared the responses of juvenile male hamsters to long photoperiods (16 h:8 h L:D), short photoperiods (10 h:14 h L:D) and short photoperiods interrupted by an equal photon pulse of monochromatic light of 320, 340, 360, 500 or 725 nm during the night. The results show that UV-A wavelengths at 320, 340 and 360 nm can regulate both reproductive and immune short-photoperiod responses as effectively as visible monochromatic light at 500 nm. In contrast, long-wavelength visible light at 725 nm did not block the short-photoperiod responses. These results suggest that both wavelengths in the visible spectrum, together with UV-A wavelengths, contribute to hamster photoperiodism in natural habitats.

Key words: *Phodupus sungorus*, ultraviolet radiation, wavelength, reproductive system, immune system, thymus, photoperiodism

Introduction

In rodent species such as the Syrian hamster (*Mesocricetus auratus*) and the Siberian hamster (*Phodopus sungorus*), exposure to short daylengths, as would naturally occur during the autumn and winter months, induces a decreased function at all levels of the reproductive hypothalamic–pituitary–gonadal axis (Hoffman and Reiter, 1965; Hoffmann, 1973; Arendt, 1995). In Siberian hamsters, it has been clearly demonstrated that this short-day inhibition of the reproductive system is correlated with a longer duration of nocturnal melatonin secretion (Carter and Goldman, 1983; Maywood et al., 1990; Bartness et al., 1993), but the precise mechanism by which the melatonin signal connotes daylength remains unknown (Gunduz and Stetson, 2001a; Gunduz and Stetson, 2001b). These and numerous other studies have established the importance of photoperiod and the secretion of melatonin from the pineal gland in regulating reproductive system activity in seasonally breeding species (Stetson and Watson-Whitmyre, 1984; Stetson and Watson-Whitmyre, 1986; Arendt, 1995).

Typically, studies on rodent reproductive photoperiodism examine the influence of changing artificial daylengths using automatically timed light:dark cycles of room illumination provided by ordinary white fluorescent or incandescent lamps. Syrian hamsters exposed to natural, outdoor autumn and winter photoperiods exhibit similar reproductive responses (Reiter, 1973). In one study, groups of age-matched Syrian hamsters were exposed to short photoperiods in either the laboratory (artificial light) or an outdoor environment (natural light) for 11 weeks. The animals exposed to natural photoperiods exhibited reproductive inhibition significantly faster than the animals kept under artificial light (Brainard et al., 1984). Numerous environmental differences might have accounted for the different rates of reproductive change including light intensity, light spectrum, temperature, humidity, noise, odors and the like. Follow-up studies demonstrated that both light intensity and spectrum are important determinants of short-photoperiod reproductive inhibition (Brainard et al., 1985; Brainard et al., 1986a). Surprisingly, those studies indicated that ‘non-visible’ near-ultraviolet wavelengths (UV-A) were as effective as visible wavelengths in modulating hamster reproductive status. Soon after, it was demonstrated that monochromatic UV-A light at 360 nm could rapidly suppress pineal melatonin production in Syrian hamsters, rats (*Rattus norvegicus*) and mice (*Peromyscus leucopus*) (Brainard et al., 1986b; Podolin et al., 1987; Benshoff et al., 1987; Brainard et al., 1994). Furthermore, it was shown that a daily pulse of monochromatic UV-A light at 340 nm delivered during the

night reversed the effects of short photoperiod on reproductive inhibition in Siberian hamsters (Brainard et al., 1991). These studies opened the door for further probes of the capacity of UV-A light to influence circadian physiology in rodents. Recently, it has been shown that UV-A light can phase-shift wheel-running circadian rhythms, induce expression of c-fos in the suprachiasmatic nuclei, and rapidly suppress pineal N-acetyltransferase activity (Provencio and Foster, 1995; Amir and Robinson, 1995; Zawilska et al., 1998; Sharma et al., 1998). Furthermore, the eyes of some rodent species have been shown to have specific cone photoreceptors with a maximum sensitivity in the near ultraviolet range (Jacobs et al., 1991; Jacobs and Deegan, 1994; Calderone and Jacobs, 1995; Calderone and Jacobs, 1999).

In addition to regulating the pineal–reproductive axis, photoperiod also elicits changes in the rodent immune system (Vriend and Lamber, 1973; Hoffman et al., 1985; Vaughan et al., 1987; Brainard et al., 1987; Brainard et al., 1988; Nelson and Demas, 1996; Nelson et al., 1998). In general, the immune system of many temperate rodents is enhanced during exposure to short photoperiods, which results in increased leukocyte numbers (Blom et al., 1994), increased thymus size (Mahmoud et al., 1994) and increased wound healing rates (Nelson and Blom, 1994). Yellon et al. (Yellon et al., 1999a) found that lymphocyte counts and killer cell activity in Siberian hamsters were increased during short-day exposure, but these authors also found a reduction in some other leukocyte activity. In a different study, Yellon et al. (Yellon et al., 1999b) reported that the T-cell-mediated humoral immunity is dependent upon the integrity of the pineal gland and its hormone, melatonin. Further, melatonin treatment has been found to elicit activity in macrophages, natural killer cells and T-helper lymphocytes (Angeli, 1988; Calvo et al., 1995; Garcia-Maurino et al., 1997). Whether or not the pineal gland mediates the effects of photoperiod on immune system function has yet to be determined.

The aim of the current study was to characterize which ultraviolet wavelengths are transmitted through the lens of the Siberian hamster and to probe the range of UV-A and visible wavelengths participating in the photoperiodic regulation of the reproductive and immune systems. The data demonstrate that the Siberian hamster lens transmits ultraviolet wavelengths down to 300 nm and that monochromatic UV-A wavelengths down to 320 nm can regulate both reproductive and immune responses to short photoperiod.

Materials and methods

Animals

All experiments were reviewed and approved by the Jefferson Medical College Institutional Animal Care and Use Committee to ensure that the experiments minimized any potential pain and discomfort to the experimental animals. Adult (25–30 g) and juvenile (aged 16–19 days, 11–15 g) male Siberian hamsters (*Phodopus sungorus*) were obtained from a colony at the University of Delaware. All the animals were raised in a long photoperiod (16 h:8 h L:D) prior to the onset of the experiments.

Lens transmission

Eye specimens from adult male hamsters were taken immediately after they were sacrificed by decapitation. The spectral transmittance of all samples was measured over the range 200–2500 nm using a Beckman (model UV 5240) spectrophotometer (Beckman, Palo Alto, CA, USA). Lens samples were taken by simple dissection, and the lenses were mounted between two ultraviolet-transmissible quartz plates. The mounting device applied a gentle flattening pressure to the lens surfaces that helped to reduce the focal power of the lens in the spectrophotometer beam. The lens sample was centered in the beam by use of a 1.0 mm thick opaque disk with a circular aperture of diameter 3.0 mm. The aperture was placed between the quartz plates, thereby determining the lateral and path-length dimensions of the sample. A matching aperture with a single quartz plate was mounted in the reference beam of the spectrophotometer.

Photoperiod protocol

Five sets of animals (mean ± S.E.M., 30.4±2.1 per set) were entered into five separate photoperiod studies. For each set of animals, the hamsters were randomly allocated to three groups (mean ± S.E.M, 10.1±0.4 per group) and housed 4–5 per cage and supplied with food and water *ad libitum*. These groups of animals were kept in one of three conditions for 13-14 days: a long photoperiod (16 h:8 h L:D); a short photoperiod (10 h:14 h L:D); or a short photoperiod (10 h:14 h L:D) interrupted during the night by a 15 min pulse of monochromatic light. In all conditions, lights were turned off at 21:00 h. Animals were housed in a room with lights set on a 14 h:10 h L:D cycle. Within this room, hamsters were kept in light-tight cabinets, each individually controlled by automatic timers. Each cabinet was illuminated independently and well-ventilated by fans. The daily light was produced by a broad-spectrum white light source (Vita-Lite, Duro-Test Corp., North Bergen, NJ, USA, or General Electric, Cleveland OH, USA), which provided an irradiance of approximately 250 $\mu W\,cm^{-2}$ at the animals' eye level (80 lx). After 2 weeks of exposure to these lighting conditions, the whole body masses of animals were recorded and they were killed by rapid decapitation. The thymus and testes were removed from each animal by sharp dissection and weighed.

Experimental light production and measurement

Monochromatic light pulses occurred during the middle part of the animals' dark period for 13–14 days at 02:00 h and lasted 15 min. Exposures to 320, 340, 360, 500, 725 nm were balanced to 4.08×10^{15} photons cm^{-2} to give equal photon exposures. Depending on which wavelength was being tested, the photic stimuli were produced by a 300 W tungsten lamp, a 275 W RSM sunlamp, or a 100 W quartz–halogen lamp and collimated by a set of quartz condensing lenses. The light was filtered by a glass infrared filter and a 51×51 mm narrow-band

interference filter (Oriel Corp., Stratford, CT, USA). The half-peak bandpass of the different interference filters ranged from 9 to 13 nm. Glass neutral density filters and/or fine mesh metal screens (Oriel Corp.) were used to adjust light irradiance. Exposure times were controlled by a timer connected to the light source. Irradiances of wavelengths above 400 nm were measured within the exposure chamber at the eye level of the animals with a J16 photometer/radiometer and a remote J6512 irradiance probe (Tektronix, Inc., Beaverton, OR, USA). Wavelengths below 400 nm were measured with a model 4D UV-A intensity meter with a remote probe (Solar Light Co.), a model 6A UV hazard meter with a remote probe (Solar Light Co.), or a UV-B 300 meter (Spectroline, Inc.).

Statistical analyses

Statistical analyses were performed on the body masses of each group of animals, with one-way analysis of variance (ANOVA) and a post-hoc multiple-range comparison using the Student–Newman–Keul's test. The percentage of total body mass for the thymus and paired testes was determined, and both ANOVA and multiple-range comparisons were run on these data.

Results

Lens transmission

Mean transmittance data for the lenses of Siberian hamsters are presented in Fig. 1. Lenticular infrared absorbance peaks were seen at 1450 and 1950 nm for all lenses evaluated. It is clear that the lenses transmit near-ultraviolet radiation almost as effectively as visible wavelengths. The lenticular short-wave cut-off point was 300 nm.

In each of the five photoperiodism studies, the whole body mass of animals in long photoperiods was significantly greater than the animals in short photoperiods (at least $P<0.05$). Consequently, all specific organ masses are expressed as a percentage of the total body mass, as shown in Table 1. In all experiments, the paired percentage testicular masses were significantly lower ($P<0.001$) in short-photoperiod animals than in long-photoperiod animals. In animals that received a daily pulse of low-irradiance monochromatic 320, 340, 360 or 500 nm radiation, percentage testicular masses were similar to those animals in long photoperiods. In contrast, the hamsters treated with 725 nm visible light had percentage testicular masses similar to those of animals kept in a short photoperiod. Fig. 2A illustrates the testicular responses of juvenile male hamsters to 2 weeks of photoperiod and wavelength treatment.

In all five experiments, percentage thymus mass was lower after exposure to long photoperiods than after exposure to short photoperiods. In four of the groups, animals in long photoperiods had significantly ($P<0.05$ to $P<0.001$) lower percentage thymus mass than animals in short photoperiods. In the experiment using a 340 nm pulse, there was a trend for lower percentage thymus mass, but it was not statistically significant. Animals in short photoperiods with a daily pulse of 320, 340, 360 or 500 nm monochromatic radiation had percentage thymus mass similar to those of animals in long photoperiods. In contrast, the hamsters treated with 725 nm visible light had percentage thymus mass similar to those of animals kept in a short photoperiod. Thus, all UV-A wavelengths tested modified the development of the thymus, as did the 500 nm visible stimulus, but not the longer-wavelength visible stimulus of 725 nm. Fig. 2B illustrates a sample of the thymic responses of juvenile male hamsters to 2 weeks of photoperiod and wavelength treatment.

Discussion

The data from this study demonstrate that the Siberian hamster lens transmits ultraviolet wavelengths down to 300 nm and that this transmission is nearly equivalent to that of wavelengths in the visible portion of the electromagnetic spectrum. In addition, the results show that monochromatic UV-A wavelengths at 320, 340 and 360 nm can regulate both reproductive and immune responses to short photoperiods to the same extent as monochromatic light at 500 nm. In contrast, long-wavelength light at 725 nm did not block the short-photoperiod responses of the reproductive and immune systems. These results demonstrate that near ultraviolet

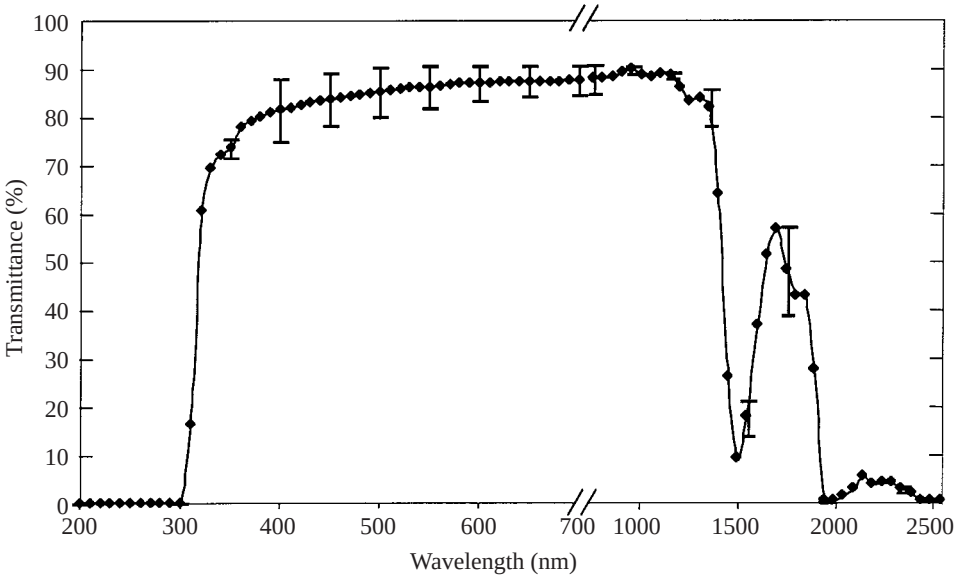

Fig. 1. Lens transmittance of ultraviolet (<400 nm), visible (400–760 nm) and infrared (>760 nm) energy in adult male Siberian hamsters (*Phodopus sungorus*). Values are means ± S.D. (N=3).

Table 1. *Mean percentage organ masses of juvenile Siberian hamsters exposed to different photoperiods*

Organ	Test wavelength (nm)	Photoperiod			Significance		
		Short	Long	Pulse	Long *versus* short photoperiod	Long *versus* pulse photoperiod	Short *versus* pulse photoperiod
Testes	320 (*N*=29)	0.11±0.01	1.90±0.08	1.97±0.21	0.001	NS	0.001
	340 (*N*=36)	0.48±0.15	1.66±0.05	1.71±0.07	0.001	NS	0.001
	360 (*N*=24)	0.20±0.01	1.96±0.11	1.39±0.29	0.001	NS	0.001
	500 (*N*=28)	0.17±0.03	1.93±0.06	1.82±0.21	0.001	NS	0.001
	725 (*N*=34)	0.36±0.12	2.17±0.07	0.63±0.22	0.001	0.001	NS
Thymus	320 (*N*=29)	0.22±0.01	0.14±0.01	0.13±0.01	0.001	NS	0.001
	340 (*N*=36)	0.18±0.01	0.16±0.01	0.15±0.01	NS	NS	0.025
	360 (*N*=24)	0.22±0.01	0.18±0.01	0.15±0.01	0.01	0.05	0.001
	500 (*N*=28)	0.22±0.01	0.16±0.01	0.17±0.01	0.001	NS	0.001
	725 (*N*=34)	0.18±0.01	0.15±0.01	0.18±0.01	0.05	0.025	NS

Values are means ± S.E.M. NS, not significant.

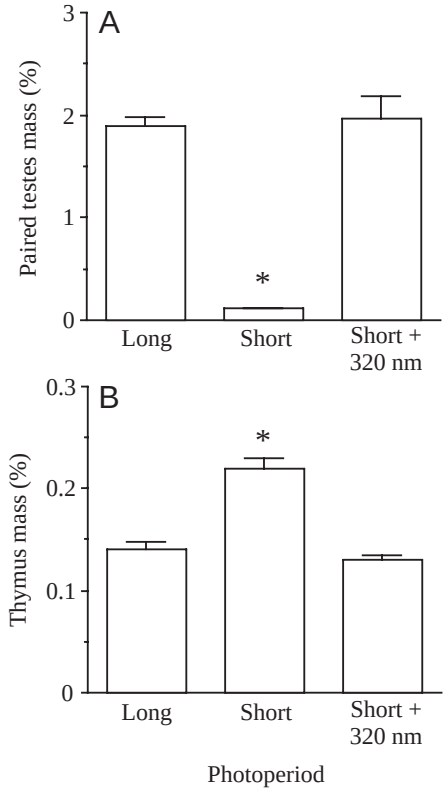

Fig. 2. The effects of a daily pulse of monochromatic ultraviolet radiation at 320 nm (Short + 320 nm) on the reproductive and immune systems of developing juvenile male hamsters. (A) Mean testes mass (%) of animals exposed to a long photoperiod (16 h:8 h L:D), a short photoperiod (10 h:14 h L:D), or a short photoperiod with a daily 15 min pulse of monochromatic UV-A light at 320 nm during the middle of the night. (B) Mean thymus mass (%) of the same animals. Values are means ± S.E.M. (*N*=29). An asterisk indicates a significant difference ($P<0.001$) from the long-photoperiod value.

radiation is capable of regulating the Siberian hamster's photoperiodic reproductive and immunologic responses.

Classically, ultraviolet radiation has been considered to be 'non-visible' to mammals. Indeed, most controlled, laboratory research on the regulation of circadian and circannual rhythms in mammals employed lamps that principally emit 'visible' light (Aschoff, 1981; Binkley, 1990). By international convention, 'visible' electromagnetic energy extends from 760 nm to 380 nm, while ultraviolet radiation is divided into three major bandwidths: UV-A, 400–315 nm; UV-B, 315–280 nm; and UV-C, 280–200 nm (Commission Internationale De L'Eclairage, 1987). The data reported here suggest that these definitions are anthropomorphic and may be less relevant to the photic environment of Siberian hamsters. In terms of photoperiodic responses, hamsters responded to the monochromatic UV-A stimuli as if they were 'visible', while they did not respond to the 'visible' 725 nm stimulus.

Photoperiodism in rodents depends on light stimulation of the retina (Aschoff, 1981; Binkley, 1990; Arendt, 1995). Hence, for environmental illumination to be an effective photoperiodic stimulus, it must be transmitted through the clear media of the eye. It is generally accepted that the cornea, aqueous humor and vitreous humor of mammals transmit wavelengths down to at least 300 nm (Boettner and Wolter, 1962; Mikesell and Maher, 1978; Maher, 1978; Barker, 1979; Chou and Cullen, 1984). Studies with rodents showed that the lenses of at least three mammalian species, Syrian hamsters (*Mesocricetus auratus*), long Evans hooded rats (*Rattus norvegicus*) and North American white-footed mice (*Peromyscus leucopus*), also transmit ultraviolet radiation as low as 300 nm to the retina (Brainard et al., 1991; Brainard et al., 1994). The Siberian hamster transmittance data presented here are consistent with those earlier observations. Rat lenticular data has been reported, however, which appears to show greater attenuation of short wavelength transmission in the 300–330 nm region (Gorgels and van Norren, 1992). The source of differences between these published studies is not known.

Lenticular long-wavelength absorbance in Siberian hamsters and other nocturnal rodents is similar to that observed in other mammalian species (Boettner and Wolter, 1962; Maher, 1978; Chou and Cullen, 1984; Lerman, 1984). The data reported here demonstrate that the Siberian hamster lens transmits wavelengths as long as approximately 2500 nm, with second and third smaller peaks at approximately 1700 and 2200 nm, respectively. This transmission of long wavelengths has been reported in rats and Syrian hamsters (Brainard et al., 1991; Brainard et al., 1994). Currently, it is not known if the transmission of wavelengths above 800 nm is functional in rodents. In contrast, the short-wavelength lenticular transmittance of Siberian hamsters and other nocturnal rodents extends much farther into the UV-A and UV-B ranges (300 nm) than is seen, for example, in the lenses of diurnal squirrels or older adult humans, which cut off transmission below 400 nm (Boettner and Wolter, 1964; Chou and Cullen, 1984; Brainard et al., 1997). The lenses of non-human primates and young humans also absorb strongly around 400 nm but, unlike squirrels, there is a small window of transmittance which peaks at 320 nm and closes at 300 nm (Boettner and Wolter, 1964; Maher, 1978; Brainard et al., 1997). This absorbance of short-wave energy is principally due to the aromatic amino acids and DNA in the lens and to yellow, non-protein components that specifically absorb in this region (Cooper and Robson, 1969a; Cooper and Robson, 1969b; Dillon and Atherton, 1990). That hamster, rat and mice lenses do not absorb wavelengths between 300 and 400 nm is probably related to the absence of specific absorbers in the lenses of these nocturnal species.

In the Siberian hamster lens data, the overall lenticular transmittance values appear to be slightly reduced in the central region of the spectrum because of the inherent difficulties in mounting small, high-power rodent lenses in front of a spectrophotometer beam. This makes it difficult to accurately estimate the total visible and ultraviolet energy transmitted to the retinal surface in the in vivo condition. Assuming that the smaller rodent lens transmits within its transparent spectral region in a manner similar to larger, easier-to-measure lenses, such as those from rabbits or humans, it is likely that the total lenticular transmittance in the rodent exceeds 90 % over the range 310–1350 nm, with a cut-off at 300 nm (Barker, 1979; Algvere et al., 1993; Boettner and Wolter, 1962; Brainard et al., 1997).

It is well documented that short-photoperiod exposure inhibits reproductive physiology in Siberian hamsters (Hoffmann, 1973; Carter and Goldman, 1983; Maywood et al., 1990; Bartness et al., 1993; Gunduz and Stetson, 2001a; Gunduz and Stetson, 2001b). The initial observation that nocturnal pulses of monochromatic UV-A light could interrupt the short photoperiod inhibition of testicular growth in juvenile Siberian hamsters (Brainard et al., 1991) is significantly extended by the data reported here. Consistently, exposure to equal photon densities of monochromatic 320, 340, 360 and 500 nm light inhibited testicular growth in juvenile hamsters. Similarly, these same monochromatic stimuli stimulated thymus growth in the hamsters. The photoperiod-induced testicular mass changes are more dramatic (approximately 700 %) than the changes in thymus mass (approximately 30 %). Thus, as shown in Table 1, the statistical significance associated with photoperiod-induced changes in thymus mass are not as consistent as those for the testes mass. More important than gross morphological changes, however, are the functional changes that occur with decreased thymus mass. Specifically, short-photoperiod exposure in Siberian hamsters not only increases thymus mass, but also influences selected cell-mediated immune functions such as increased lymphocyte proliferation, enhanced natural killer cell activity, decreased phagocyte activity, decreased oxidative burst activity by granulocytes and monocytes, and decreased immunoglobulin production by T cells (Yellon et al., 1999a; Yellon et al., 1999b).

The traditional means of identifying a photopigment responsible for mediating any photobiological response is to determine the action spectrum for that response (Smith, 1989; Coohill, 1999). As a prelude to determining the action spectrum for visible and ultraviolet regulation of photoperiodism in hamsters, it was useful to probe the spectral range for that response. The studies described above demonstrate that hamsters have diminished sensitivity to the red portion of the visible spectrum. Unlike the other wavelengths in the visible and ultraviolet portions of the electromagnetic spectrum, the ‘red’ 725 nm stimulus in this study at 4.08×10^{15} photons cm^{-2} was not strong enough to elicit a photoperiodic response in Siberian hamsters. The reduced sensitivity of the circadian and neuroendocrine systems to red wavelengths is well established for hamsters and other rodents, but it should be noted that rodents do retain a sensitivity to long-wavelength light if the stimulus is sufficiently strong (McCormack and Sontag, 1980; Vanecek and Illnerova, 1982; Broker et al., 1990; Knapp, 1989; Sun et al., 1993; Poeggler et al., 1995). Thus, significantly higher intensities at 725 nm would ultimately be likely to impact photoperiodic responses in Siberian hamsters. Ultimately, full fluence-response curves need to be established for each of the wavelengths used in this first study.

Nearly all studies on the effects of different wavelengths on hamsters, rats and mice suggest that wavelengths in the blue and green portion of the spectrum have the strongest impact on circadian and neuroendocrine regulation (for a review, see Brainard et al., 1999). In considering the potential photopigment/photoreceptor cell type(s) that transduce photic information for photoperiodism, it should be noted that the rodent retina contains both cone and rod photoreceptors, and species are diverse in type and distribution of retinal photoreceptors (Rodieck, 1998). It is possible that a specific ultraviolet-sensitive photoreceptor cell is responsible for mediating the photoperiodic responses evoked by ultraviolet radiation in this study. Indeed, recent studies using electroretinogram sensitivity and behavioral task discrimination indicate that a variety of rodent species, including the Siberian hamster, have ultraviolet-specific photoreceptors that mediate visual sensitivity (Jacobs et al., 1991; Jacobs and Deegan, 1994; Calderone and Jacobs, 1995; Calderone and Jacobs, 1999). It

remains uncertain, however, whether the ultraviolet cone cells that support rodent visual responses necessarily mediate non-visual photoperiodic responses. Experiments on animals with hereditary or light-induced retinal degeneration have raised the possibility that neither the rods nor the cones used for vision participate in light-induced melatonin suppression, circadian locomotor phase-shifts or photoperiodic responses (Pevet et al., 1984; Webb et al., 1985; Goto and Ebihara, 1990; Foster et al., 1991; Provencio and Foster, 1995). Furthermore, bilateral removal of the eyes from rodless, coneless transgenic mice abolished light-induced circadian phase-shifting and acute melatonin suppression (Lucas and Foster, 1999; Freedman et al., 1999). Thus, it appears that phototransduction for circadian and neuroendocrine regulation occurs in the eye, but the specific photoreceptor cells that mediate these effects remain to be determined.

It is reasonable to ask whether laboratory regulation of photoperiodism by ultraviolet stimuli has any relevance to rodents in their natural habitats. In terms of the reproductive and immune responses to monochromatic UV radiation, Siberian hamsters responded to three different UV-A wavelengths at 4.08×10^{15} photons cm^{-2}. There are pronounced daily and annual fluctuations in solar ultraviolet radiation at ground level (Frederick et al., 2000). Throughout the year, irradiances of environmental UV-A light at the earth's surface 20 min before sunrise and 20 min after sunset are considerably higher than the irradiances of UV-A light required to modulate photoperiodic responses. Since hamsters emerge from their burrows during both daylight and twilight hours, it is likely that wavelengths in the 'visible' spectrum, together with UV-A wavelengths, contribute to hamster photoperiodism in natural habitats. Thus, shifts in the total photic environment due to fluctuations caused by seasonal change, weather or depletion of the stratospheric ozone layer may be important to the ecology of the Siberian hamster.

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