Phototactic Behavior of Nocturnal and Diurnal Spiders: Negative and Positive Phototaxes

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ABSTRACT—Phototactic behaviors of the garden spider *Araneus ventricosus* and the jumping spiders *Menemerus confusus* and *Hasarius adansoni* were examined as they walked on a Y-maze globe. On both dark- and light-backgrounds, *Araneus*, a nocturnal web spider, tended to turn at Y-arms away from a test light given to the eyes (negative phototaxis), but *Menemerus* and *Hasarius*, diurnal hunting spiders, tended to turn toward the light (positive phototaxis). *Araneus* tended to turn transiently toward the light after the cessation of background illumination.

INTRODUCTION

Phototactic behavior of tethered orb weaving spiders which walked on a Y-maze globe has been examined (Yamashita and Tuji, 1987; Yamashita, 1987, 1992). Yamashita and Tuji (1987) showed that on a dark- background, the orb weaving spiders, *Argiope amoena* and *Nephila clavata*, tended to turn at Y-arms directed away from a test light given to the eyes (negative phototaxis). On a light-background, however, the spiders tended to turn toward the test light (positive phototaxis). When small background illumination was presented to only a portion of the eyes, the spiders showed a negative phototaxis. On the other hand, when the brain was illuminated through the cuticle covering it via a light guide touched onto the central part of the prosoma just above the brain, the spiders showed a positive phototaxis to the test light. Yamashita and Tuji (1987) concluded that extraocular photoreceptors in the brain control the phototactic behavior of these spiders. In addition, Yamashita (1987) reported that *Argiope* also responded positively to the light for a short period after the dimming of light.

Argiope and *Nephila* appear to be active both during the day and night; they stay in the hubs of their webs and attack prey animals throughout the day. In the present study, we examined the phototactic behaviors of the garden spider *Araneus* and the jumping spiders *Menemerus* and *Hasarius*. *Araneus* constructs its web every day after sunset and puts it away before sunrise, i.e., *Araneus* is active only at night. *Menemerus* and *Hasarius* are typical diurnal hunting spiders and a number of their behavioral activities are initiated by visual stimuli (cf. reviews by Forster, 1985; Land, 1985; Yamashita, 1985). In this paper, we report that *Araneus* shows a negative phototaxis, but *Menemerus* and *Hasarius* show a positive phototaxis on both dark- and light-backgrounds.

MATERIALS AND METHODS

The animals used in this study were female garden spiders, *Araneus ventricosus*, and male and female jumping spiders, *Menemerus confusus* and *Hasarius adansoni*. These animals were collected in open fields. The body lengths of *Araneus*, *Menemerus* and *Hasarius* were about 25–30 mm, 7–9 mm and 7–9 mm, respectively. Most spiders were exposed to the normal day and night cycle of Fukuoka. In some experiments, spiders were maintained on a photoperiod of 12 hr light and 12 hr darkness for a few days.

The methods are similar to those described previously (Yamashita and Tuji, 1987). The spider was held rigidly in space and was given a Y-maze globe to hold. For test stimuli, a light beam emitted by a tungsten filament lamp or a Xenon arc lamp was passed through a heat-absorbing filter and focused onto the end of a light guide. The exit of the light guide was aimed at the right eyes 45° clockwise or at the left eyes 45° anticlockwise to the body axis. The light spot had a subtended aperture of about 1.5° for the garden spider and about 3.5° for the jumping spider. The intensity of illumination was adjusted by calibrated neutral density filters and wedges. The unit intensity (log I = 0.0) of the test light was about 300 lux at the preparation. Background illumination was given by scattered light from a tungsten lamp placed over the spider. The intensity was controlled by changing the voltage. For illumination of the brain of *Araneus*, a light beam emitted by a tungsten lamp was passed through a heat-absorbing filter and calibrated neutral density filters, and focused onto one end of a light guide 2 mm in diameter. The other end of the light guide was joined onto the central part of the prosoma just above the brain.

The turning reaction (TR) was defined as $P - N / P + N$, where P is the number of turns at Y-arms directed toward the test light, and N is the number of turns directed away from the light.

To examine phototactic behavior to constant light, spiders were adapted to each test light or background light for at least 10–20 min. In most cases, spiders made 100 turns at Y-arms for each test, 50 during illumination of the right eyes and 50 during illumination of the left eyes. Successive illumination of the right and left eyes were performed in order to compensate for side preferences independent of visual stimulation. When spiders showed little spontaneous walking

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activity, gentle airpuffs or tactile stimuli were given arbitrary to facilitate their walking activity (cf. Fig. 6).

RESULTS

Phototaxis of garden spiders

In Fig. 1, the TRs of three garden spiders on a dark-background are plotted against the relative intensity of the test light. The spiders tended to turn at Y-arms away from the test light and this tendency became stronger as the stimulus intensity increased. The mean value of TRs at log I = − 1.0 for five spiders was − 0.70 ± 0.14 (SD). It is obvious that garden spiders show a negative phototaxis on a dark-background.

Figure 2 shows three intensity-TR curves obtained from a single spider on a dark-background, on a light-background of 600 lux and during illumination of the brain. On the light-background, TR at each intensity decreased compared to that on the dark-background. The intensity-TR curves for dark- and light-backgrounds are approximately parallel along the abscissa, suggesting that the decrease in TR on the light-background may be simply due to light-adaption of the eyes. During illumination of the brain, TRs decreased slightly compared to those for the dark-background. The decrease also seems due to light-adaptation of the eyes since the light given to the brain diffused and part of the light reached the eyes (cf. Yamashita and Tuji, 1987). Under steady light conditions, on both dark- and light-backgrounds, and during illumination of the brain, all garden spiders examined responded negatively to the light directed at the eyes.

After the cessation of background illumination, however, we observed that garden spiders tend to turn transiently toward the test light (Fig. 3). In this figure, background illumination of 600 lux was presented for 30 min. Just before the cessation of the background illumination, TR was about − 0.07, i.e., on
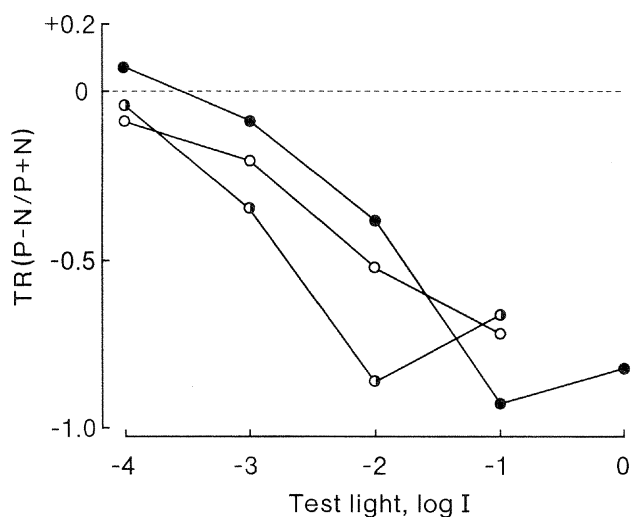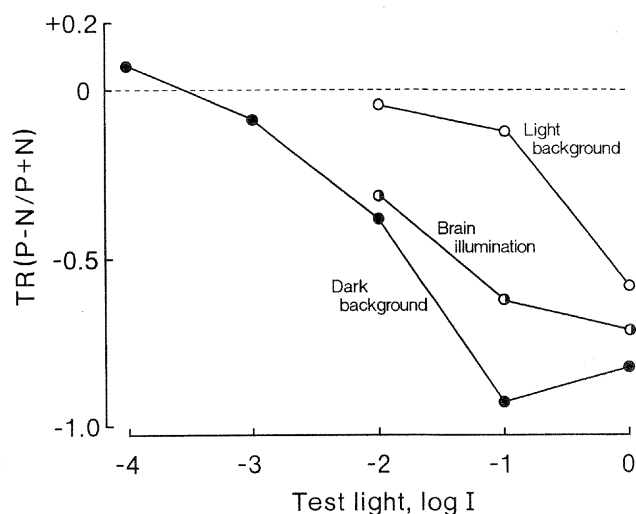

Fig. 2. Effect of background illumination and illumination of the brain on phototactic behavior. Three curves were obtained from a single garden spider. The curve for the dark-background was the same as one curve shown in Fig. 1. The intensity of background illumination on the eyes and that of brain illumination at the output of the light guide were about 600 lux.
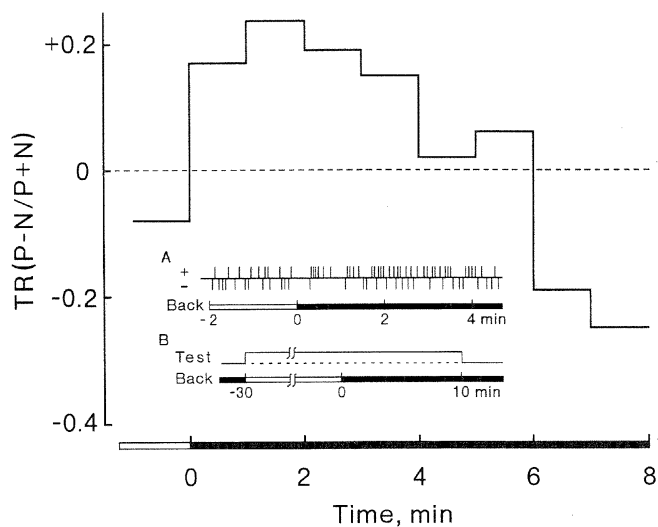

Fig. 3. Phototactic behavior after the cessation of background illumination. The mean value of TRs for three spiders is plotted against the time after the cessation of background illumination. TR was averaged every minute. Each spider was tested at intervals of over three hours for two or three days. Each spider made a total of about 20 – 40 turns each minute. The intensity of the test light was log I = − 1.0. (Inset A) An example of a test. Upward (+) and downward (–) deflections of the trace indicate that the garden spider made turns at Y-arms toward and away from the test light, respectively. (Inset B) Schematic drawing of the background illumination and the test light. The test and background lights were turned on simultaneously, and the test light was turned off about 10 min after the cessation of the background light.

Fig. 1. Phototactic behavior for three garden spiders on a dark-background. The turning reactions (TR = P − N / P + N) for individual spiders are plotted against the relative intensity of the test light.

a 600 lux background, the spiders responded somewhat negatively to the test light (cf. Fig. 2). After the cessation of background illumination, TR increased to about + 0.2 and then decreased gradually with time. TR obtained for 7–8 min after the cessation of background illumination was about − 0.25.

Phototaxis of jumping spiders

We could not find any significant difference in phototactic behavior between *Menemerus* and *Hasarius*. The mean values of TRs to the test light of log I = − 0.78 for eight *Menemerus* and six *Hasarius* on a dark-background were + 0.24 ± 0.11 (SD) and + 0.21 ± 0.06, respectively. Figure 4 shows the mean intensity-TR curve for eleven jumping spiders on a dark-background (closed circles) and that for three jumping spiders on a light background of 50 lux (open circles). TR increased as the stimulus intensity increased on both dark- and light-backgrounds. In all cases examined, we never observed jumping spiders showing a clear negative phototaxis. We, therefore, conclude that jumping spiders show a positive phototaxis on both dark- and light-backgrounds, although the positive tendency was weak compared to the negative tendency for *Araneus* (cf. Fig. 1). In addition, we did not observe marked transient changes in TR after the cessation of background illumination as observed for *Araneus* (cf. Fig. 3). In jumping spiders, selective illumination of the brain was not performed since they were too small.

DISCUSSION

Yamashita and Tuji (1987) reported that *Argiope* and *Nephila* show a negative phototaxis on dark-backgrounds and
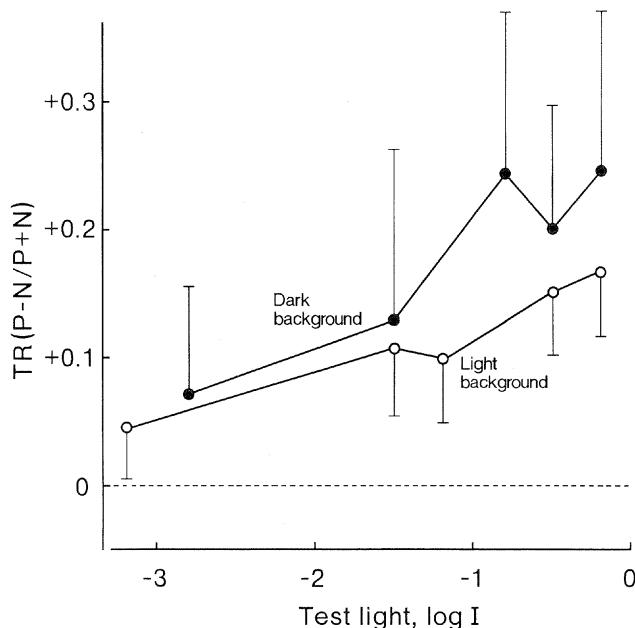

Fig. 4. Average intensity-TR curve for eleven jumping spiders on a dark-background and that for three jumping spiders on a light-background. Vertical lines indicate only one side of standard deviation.

show a positive phototaxis on light backgrounds. In the present study, we observed that the garden spider *Araneus* shows a negative phototaxis, and the jumping spiders *Menemerus* and *Hasarius* show a positive phototaxis both on dark- and light-backgrounds. The phototactic behavior of spiders should be closely related to light conditions during their active periods.

Yamashita (1987) reported that *Argiope* tended to turn toward the light for about 0.3-2 min after the dimming of light. In the present study, we observed that *Araneus* tended to turn toward the light for about 4-6 min after the cessation of background illumination. The difference in time courses may be due to the difference in light conditions. For *Argiope*, reductions in light intensity were achieved by turning off one of the two test lights presented to the right and left eyes (Yamashita, 1987). The lighter (illumination by two lights) and the darker (illumination by one light) periods were 2-5 and 2-4 min, respectively. The illumination cycle was repeated as long as each spider showed walking activity. In the present study, background illumination of 600 lux for 30 min was presented at intervals of over 3 hr.

Photoreceptor responses in the eyes of *Argiope* are controlled by efferent optic nerve signals, which indicates a diurnal periodicity under a constant darkness (Yamashita and Tateda 1978, 1981; Yamashita, 1985, 1990; Yamashita and Arita, 1995). Yamashita and Tateda (1983) found that the frequency of efferent impulses in the optic nerve increased by illumination of the brain, but decreased during illumination of the eyes. Simultaneous illumination of the eyes and the brain produced impulse discharges, especially at higher intensities of illumination. The frequency of efferent impulses increased transiently following the diminution of light intensity striking the eyes (Yamashita and Tateda, 1983). Yamashita and Tuji (1987) reported that *Argiope* and *Nephila* tended to turn at Y-arms toward the light on light-backgrounds. The spiders also tended to turn toward the light when the brain was illuminated with a small light spot (Yamashita and Tuji, 1987) and when the light given to the eyes was dimmed (Yamashita, 1987). These authors (Yamashita and Tuji, 1987; Yamashita, 1987) suggested that the activation of efferent neurons plays a role in phototactic behavior.

In our preliminary experiments, we have recorded efferent impulses from the optic nerve of *Araneus*, although impulse frequencies varied from preparation to preparation in the dark-adapted state (cf. Yamashita and Tateda, 1981). The frequency of efferent optic nerve impulses recorded from the isolated preparation consisting of the brain and optic nerve decreased during illumination of the brain (Fig. 5). The observation shows that photosensitive neurons are present in the brain of *Araneus*, although we did not determine whether the efferent neurons are directly photoinhibitory or not. In contrast, the efferent neurons of *Argiope* are directly photoexcitative (Yamashita and Tateda, 1983). We have also observed that the frequency of efferent optic nerve impulses recorded from the isolated preparation consisting of the brain, optic nerve and eyes of *Araneus* decreased during illumination of the eyes, but increased transiently after the cessation of
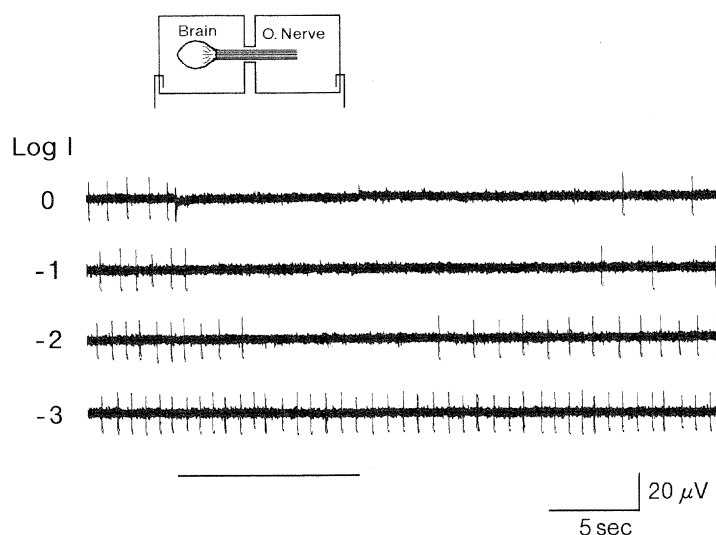
Fig. 5. Efferent optic nerve impulses in response to white light stimuli of the brain (10 sec duration at various intensities) obtained from an isolated brain-optic nerve preparation. The light intensity at log I = 0 was about 10^3 lux at the preparation. Horizontal bar: duration of illumination. (Inset) Diagram of the recording method from the isolated preparation of the brain and the optic nerve (O. Nerve) (cf. Yamashita and Tateda, 1981).
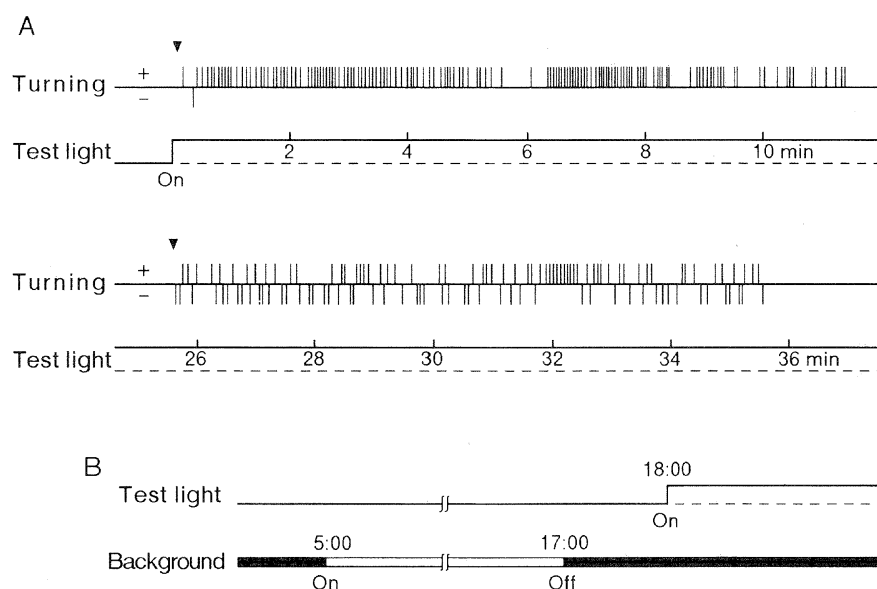

Fig 6. (**A**) An example of garden spider phototactic behavior after the cessation of background illumination for 12 hr. Upward (+) and downward (−) deflections of the trace indicate that the spider made turns at Y-arms toward and away from the test light, respectively. Arrow heads indicate tactile stimuli using a fine brush. Numbers under the solid lines indicate time after the onset of the test light in minutes. (**B**) Schematic drawing of the background light and test light.

illumination of the eyes. As shown in the present study, *Araneus* tended to turn transiently toward the light after the cessation of background illumination, but not during illumination of the brain. In *Araneus*, the activation of efferent neurons may also play a role in phototactic behavior. It is supposed that the efferent optic nerve activity of *Araneus* begins to increase in the evening, since *Araneus* showed a marked circadian oscillation of sensitivity of the eyes similar to that of *Argiope* (data not shown) (cf. Yamashita and Tateda, 1978,

1981). If the activation of efferent neuron plays a role in phototactic behavior, *Araneus* may show a positive phototaxis in the evening. An example is shown in Fig. 6. The spider was collected in open fields and maintained on a photoperiod of 12 hr light (5:00–17:00) and 12 hr darkness for two days. One hr after the cessation of the second 12 hr light period, a test light was given to the right eyes for about 6 min and then to the left eyes for about 30 min under a dark-background. For the first 11.5 min (0–11.5 min after the onset of the test light),

the spider made 139 turns at Y-arms toward the test light and only one turn away from the light. TR during this period was about + 0.99. On the other hand, during a later 10 min period (26–36 min after the onset of test light), the spider made 63 turns toward the light and 53 turns away from it. TR during this period was about + 0.09. Since then, this spider greatly reduced its walking activity. The result supports the idea that activation of the efferent neurons plays a role in phototactic behavior. However, we could not demonstrate whether spiders show a diurnal periodicity of phototactic behavior, since little spiders showed sufficient walking activity both in the morning and in the evening (cf. Yamashita, 1987). To examine the phototactic behavior, a test light must be given to the eyes. Both for *Argiope* and *Araneus*, the discharge of efferent optic nerve impulses was inhibited by illumination of the eyes (cf. Yamashita and Tateda, 1983). If the activation of efferent neurons plays a role in phototactic behavior, spiders may not show a marked diurnal periodicity of phototactic behavior.

In jumping spiders, we did not observe any marked change in phototactic behavior during and after the cessation of background illumination as found in *Argiope* and *Nephila* (Yamashita and Tuji, 1987; Yamashita, 1987). We have not observed any impulse activity in the optic nerve of jumping spiders nor any circadian change in sensitivity of the eyes. In jumping spiders, efferent neurons, which we assumed play a role in phototactic behavior, may not be present. As a result, jumping spiders may always show a positive phototaxis.

REFERENCES

Forster L (1985) Target discrimination in jumping spiders (Araneae: Salticidae). In "Neurobiology of Arachnids" Ed by Barth FG, Springer, Berlin, Heidelberg, New York, pp 249–274

Land MF (1985) The morphology and optics of spider eyes. In "Neurobiology of Arachnids" Ed by Barth FG, Springer, Berlin, Heidelberg New York, pp 53–78

Yamashita S (1985) Photoreceptor cells in the spider eye: spectral sensitivity and efferent control. In "Neurobiology of Arachnids" Ed by Barth FG, Springer, Berlin, Heidelberg, New York, pp 103–117

Yamashita S (1987) Dimming reaction of the orb weaving spider, *Argiope amoena*. Zool Sci 4: 31–35

Yamashita S (1990) Efferent optic nerve impulses in response to illumination of single eyes of orb weaving spiders. Vision Res 30: 817–821

Yamashita S (1992) Effect of monochromatic illumination of the brain on the phototactic behavior of orb weaving spiders, *Argiope amoena* and *Nephila clavata*. Zool Sci 9: 887–889

Yamashita S, Arita F (1995) Efferent control in the anterior lateral eyes of orb weaving spiders. Zool Sci 12: 385–389

Yamashita S, Tateda H (1978) Spectral sensitivities of the anterior median eyes of the orb web spiders, *Argiope bruennichii* and *A. amoena*. J Exp Biol 74: 47–57

Yamashita S, Tateda H (1981) Efferent neural control in the eyes of orb weaving spiders. J Comp Physiol 143: 477–483

Yamashita S, Tateda H (1983) Cerebral photosensitive neurons in the orb weaving spiders, *Argiope bruennichii* and *A. amoena*. J Comp Physiol 150: 467–472

Yamashita S, Tuji R (1987) Phototactic behavior of the orb weaving spiders, *Argiope amoena* and *Nephila clavata*. Zool Sci 4: 23–30