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EVIDENCE FOR IDIOTHETICALLY CONTROLLED TURNS AND EXTRAOCULAR PHOTORECEPTION IN LYCOSID SPIDERS

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ABSTRACT. During some of the intervals between bouts of pheromone-stimulated courtship display, isolated male *Rabidosa rabida* (Araneae, Lycosidae) perform a single pivot. In an investigation of the control of this turning behavior, males were tested under four conditions. Two of these were visual, a uniform environment or one with images, and two were non-visual, all eyes occluded or dim red lighting. The turning angle and the tendency to change the direction of turning were measured for the first three conditions, and no significant differences were found. This suggests that the turns are controlled idiothetically. Another parameter, the tendency to perform the turns, was reduced under dim red light but not in blinded spiders under white light, the latter suggesting the occurrence of extraocular photoreception.

When animals organize their behavior with respect to spatial features, they use information obtained from external directing stimuli (allothetic orientation) or from internal sources (idiothetic orientation). The latter may depend either on proprioceptive information or on central nervous system (nonsensory) programs that contain the necessary information for spatial execution of movements (Schöne 1984). The present study deals with the question of whether rotational locomotion that occurs during courtship behavior in isolated male lycosid spiders is influenced by visual stimuli or is under idiothetic control.

The display of *Rabidosa rabida* (Walckenaer) occurs in discrete bouts. In each bout the palps are waved in alternation, and then the right or left leg I is extended coincident with palpal-produced sounds. Both of the latter elements end abruptly in synchrony. A pause follows, during which time a receptive female, if present, signals her response. Thus, the male's distinct bouts of display alternate with inter-bout intervals, providing a basis for reciprocal signaling between the sexes.

When this species' display was quantitatively analyzed (Rovner 1968), the data were obtained from males in the presence of females. However, when males in isolation are stimulated to display by contact with the female's sex pheromone, an additional behavior occurs. During some of the inter-bout intervals, such males perform a single pivoting turn. Rovner (1991) hypothesized that this rotational locomotion represents a component of a local search pattern. Apparently, it is added to the behavior of a male in the courtship mode if he has failed to detect a responding female during the early phase of courtship.

Since turning behavior in animals can be influenced by goal-related images or by the level of illumination (Schöne 1984), I examined whether such visual input plays a role in the inter-bout turning behavior of isolated male *R. rabida*. I tested spiders in well-lit arenas with or without fixed images and also tested them under non-visual conditions: in darkness (dim red light) or after occlusion of the eyes.

METHODS

Fifty male and 10 female *Rabidosa rabida* (formerly *Lycosa rabida*) were collected as penultimate instars in early July 1989 in a field in Athens County, Ohio. Spiders were not used until 1 week or more after the final molt. Methods of maintenance and laboratory conditions during testing were described previously (Rovner 1989).

The testing arena was a glass bowl with a sloping wall, on the inside of which a coat of flat, pale green, non-toxic paint had been applied to provide a uniform, non-reflecting surface. The bottom was covered with a cardboard disk, over which was placed a pale green sheet of paper 11.3 cm in diameter (about 100 cm^2). The latter was replaced with a fresh sheet for each test, so that silk or chemicals deposited on the substrate by one spider could not remain to influence subsequent individuals. A vertical cardboard barrier visually isolated the arena from my location.

For most test conditions, non-directional illumination was provided by a 32 W, soft-white, circular fluorescent bulb centered over the arena (height = 50 cm above the arena floor). The level of illumination at the arena floor was about 700 lux (Gossen Luna-Pro meter), comparable to the light level in a deciduous forest understory on a sunny day.

For a test condition without visible light being available to the spiders, a dim red light was provided by Kodak Safelight (No. 1 filter; 15 W incandescent bulb) placed 20 cm above the arena floor. The filter passed wavelengths ≥ 610 nm. Even under bright white light, the sensitivity of the largest eyes (posterior median) of wolf spiders falls off sharply above 550 nm, especially if the spiders are light-adapted when tested (DeVoe et al. 1969), as was the case in the present study. The single window in the laboratory was covered with opaque material, and tests under this condition were conducted after dark in the late evening. With this arrangement, a very low level of red light (about 2–4 lux) reached the arena floor, just sufficient for my direct observations but not adequate for monitoring or recording by video. Consequently, only the number of display bouts and turns (not turning angles) was included in the data for this test condition.

To determine whether the dim red light condition insured total darkness for the spiders, I ran a preliminary check on 20 males in the following manner. Pairs of males were vibrationally isolated in separate cages that allowed visual contact (Rovner 1989) and were observed under the dim red light until one of the males had initiated walking and performed three passes across his cage. None of the males showed a response to a walking male under this condition. They subsequently oriented and showed courtship display to such a stimulus after I switched on a white light (an exposed 10 W bulb 25 cm above the cages that provided about 300 lux illumination). On this basis, the dim red light was judged satisfactory for insuring darkness.

Observations and data recording in the three test conditions run under white fluorescent light were done with the aid of a video camera (JVC model GX-8NU), a remote-controlled videocassette recorder (Sony model SL-HFR70), and a video monitor. A character generator (JVC model CG-C7U) provided an on-screen stopwatch (reading to 0.1 s) and titles identifying each test. The video recorder was located on a separate table 1.2 m from the testing arena to prevent possible vibratory stimulation. The camera faced obliquely upward toward a front-silvered mirror clamped above the testing arena at a 45° angle to the floor. This gave a dorsal view of the spider, essential for later measurement of turning angles (by use of a protractor placed over the still frame on-screen). Due to limitations imposed by the resolution of the video image, I could accurately measure angles only to the nearest 5°.

Each male to be tested was transferred in a plastic vial from its home cage to the arena. I allowed the spider to slide gently onto a centrally located stimulus source, a square section (6.25 cm^2) of a larger piece of paper that had served as the floor covering in a female's cage for a number of days. I then sat out of sight of the arena and viewed the monitor. As soon as the male began courtship display, I remotely activated the video recorder and kept it running for the next 10 min. Twenty males were tested only once, and 30 males were used twice, i.e., in two of the four test conditions, mixed through all of the treatments. When a male was used twice, the tests were separated by several days, so as to achieve a reasonable level of independence.

The four conditions examined were: (1) fixed images on arena wall, (2) uniform arena wall, (3) dim red light, and (4) occluded eyes. While tests under the red light condition were run only in the late evening, those under the other three conditions were run throughout the day and evening. Twenty males were tested under each condition.

The stimuli used for testing the influence of images consisted of two identical silhouettes of the front view of female wolf spiders, comparable to shapes presented to salticid spiders by various workers, including Crane (1949), but remaining fixed rather than being moved like those usually used for salticids. I attached the images to the arena wall opposite each other and at floor level so as to simulate the appearance of female conspecifics resting at the arena's edge. I used more than one image to insure that the male had an easy opportunity to pick up the potential stimulus within his visual field soon after his entry into the arena, no matter which direction he faced initially. The maximum distance from the spider to an image was well within the range of detectability, based on data from a previous study (Rovner 1989).

To occlude the eyes, I covered them with two,

Table 1.—Inter-bout turning behavior in courting male *Rabidosa rabida*. There were no differences among turning angles (Kruskal-Wallis, $H_c = 1.149$) or series lengths of turns in the same direction ($H_c = 1.316$). Data were based on 10 males/condition.

Condition	Number of turns	Turning angle (degrees)	Series of turns in same direction	Turning angle × series length
Fixed images	70	62 ± 45.9	2.6 ± 2.21	155°
Uniform wall	85	67 ± 55.3	2.8 ± 1.81	201°
Occluded eyes	107	61 ± 40.2	2.9 ± 1.90	183°
Grand mean ± SD		63 ± 47.0	2.8 ± 1.96	176°

separately applied, coats of water-based enamel (Top Color Hobbylack, Pelikan AG). That this insured complete occlusion had been established previously (ibid.).

Data on turning angles were based on the magnitude of each turn, irrespective of direction. Where appropriate, I present these and other data as $\bar{X}$ ± SD. Analyses of data involved Kruskal-Wallis tests (corrected for ties) and *t*-tests of arcsine-transformed percentages (Sokal & Rohlf 1969).

RESULTS

Occurrence of turns.—During courtship, an "inter-bout interval" that was 6.7 ± 1.51 s in duration followed each bout of display, and there was a mean of 3.0 ± 0.83 display bouts/min. After an early phase of courtship in which no locomotion occurred during the inter-bout intervals, the male pivoted in place during 21.4% of the subsequent inter-bout intervals. (A small amount of forward locomotion sometimes occurred during an inter-bout interval; however, the nature of such linear locomotion was not addressed in the present study.) A pause always preceded inter-bout locomotion, during which time a receptive female, had one been present, would have performed her receptive display. Turning never occurred during the male's bouts of courtship display.

Table 2.—Tendency of male *Rabidosa rabida* to perform inter-bout turns. Data were based on 20 males/condition. (For $t = 1.96$, $P = 0.05$.)

Condition	Total turns	Total bouts	Percent	*t*	*P*
Fixed images	121	599	20.2	1.93	>0.05
Uniform wall	157	632	24.8	3.15	<0.01
Red light	93	537	17.3	2.31	<0.05
Occluded eyes	145	638	22.7		

Turning angle.—Turns resulted from forward steps by the legs of one side of the spider and reverse steps by the contralateral legs. (Some spiders occasionally made very small turns of 15° or less, resulting from a single remotion of one or two anterior-most ipsilateral legs. Such cases lacking bilateral appendage involvement were not included in the analyses.) Turning angle, which had a mean of 63 ± 47.0°, was independent of the presence or absence of fixed, spider-like images and of whether the eyes were occluded or not (Table 1).

Turning direction.—Viewed dorsally, turns were either clockwise or counterclockwise, with both directions equally represented in the data, i.e., no handedness. Although in about one-third of the cases a directional change occurred after only one turn in the other direction, in the majority of cases the spiders performed a series of turns in one direction, then a series in the other direction. Since turns only occurred during inter-bout intervals and only during about a fifth of these intervals, it must be kept in mind that a "series" of turns involved behavioral events separated by time and by other activity. The number of turns in a series of unidirectional turns ranged from two to eight ($\bar{X}$ = 2.8 ± 1.96) and was independent of the presence or absence of fixed, spider-like images and of whether the eyes were occluded or not (Table 1).

Turning tendency.—The percentage of courtship bouts followed by turns was regarded as an indicator of turning tendency (Table 2). Comparisons of arcsine-transformed percentages between treatment groups revealed significant differences in two cases: (1) Spiders tested under red light turned less often than those under white light in uniform arenas. (2) Blinded spiders under white light turned more often than untreated spiders under red light. A difference just shy of significance was also noted: Untreated spiders exposed to fixed images turned less often than those surrounded by a uniform wall. Some of the former did maintain an initial orientation toward an image for a period of time after their introduction to the arena.

DISCUSSION

Orientation behavior in animals can involve a mechanism that relies on external input or can be controlled entirely by an internal mechanism (Schöne 1984). Data obtained in the present study suggested that pivoting turns occurring during courtship in isolated male lycosid spiders can be performed independently of external stimuli. The methods eliminated vibrational cues since no female was present; and directional lighting was avoided as well. Testing in the presence or absence of fixed images and testing under greatly different illumination levels were the approaches used to determine the possible influence of certain visual stimuli on the orientation behavior being studied.

When provided with fixed, spider-like images, male *R. rabida* did not show significant differences in either turning angles or turning series lengths from those of spiders in a uniform environment. Such data support the view of Homann (1931), who stated that the eyes of wolf spiders are adapted for the detection of movement. However, turning tendency was almost significantly less for spiders exposed to the fixed images compared to those in a uniform environment. This resulted from some spiders having temporarily held an orientation toward an image detected at the time of introduction to the arena. Crane (1949) also observed this occasionally in salticids, which usually do not respond to a fixed image. She suggested that when a spider is dropped into the arena "the visual effect to the spider may be similar to that obtained when the stimulus is moving".

The size of inter-bout turns was the same in *R. rabida* with occluded eyes as in untreated individuals, which suggests that these turns are controlled endogenously. Such self-steered turns are well known in various arthropods and were thoroughly analyzed in a series of studies on courtship turning in the cockroach *Blattella germanica* (Bell et al. 1978; Bell & Schal 1980; Franklin et al. 1981). However, one cannot be completely certain that turning behavior in any arthropod is under idiothetic control until tests employing Helmholtz coils are used to eliminate the remote possibility of geomagnetic orientation (Havukkala & Kennedy 1984).

The tendency of male *R. rabida* to turn during the inter-bout interval was affected by the level of illumination. Spiders under dim red light had a lower turning tendency than that of spiders under white light in uniform arenas and had the lowest numbers of courtship bouts and inter-bout turns of all groups. Interestingly, Frings (1941) had found that *R. rabida* became less active ("akinetic") under reduced illumination; and he judged this to be the reason (rather than negative phototaxis) that the spiders ended up in the shaded chamber of a choice box.

If male *R. rabida* have a reduced level of inter-bout turning under dim red light, why then did the spiders which also seemingly experienced complete darkness due to occlusion of the eyes show the same turning tendency as untreated spiders under white light? Interestingly, Kapoor (1971) found that blinded pumpkinseed fish responding to different levels of illumination showed changes in turning angle like those of untreated fish, and he noted that the fish's pineal photoreceptor can mediate such responses. Recent electrophysiological studies by Yamashita (1986) revealed that efferent neurons in the brain of two species of araneid spiders were sensitive to light. The behavioral data described here for *R. rabida* raise the possibility that extraocular photoreception also occurs in lycosid spiders, an hypothesis that requires electrophysiological confirmation in a future study.

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