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The Role of Sensory Receptors in the Predatory Behavior of the Brown Tree Snake, *Boiga irregularis* (Squamata: Colubridae)

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The brown tree snake (*Boiga irregularis*) is indigenous to parts of coastal Australia, New Guinea, and the Solomon Islands (McCoy, 1980; Cogger, 1983). It can be found in a variety of habitats (Fritts, 1988), but it is arboreal and most common in primary and secondary growth forests (Savidge, 1986, 1987; Fritts et al., 1987). Its dentition is usually referred to as "rear fanged," in which one or two posterior maxillary teeth are enlarged and bear on their labial faces an open groove associated with a connecting duct from Duvernoy's gland. The snakes appear to feed opportunistically: stomach and intestinal content analyses reveal a diet of birds and their eggs, lizards and their eggs, and small mammals (Savidge, 1988). The diets of males and females are the same, but medium to large snakes (over 120 cm SVL) tend to consume a larger proportion of birds, bird eggs, and mammals (Savidge, 1988). They are considered nocturnal in their natural habitat (Fritts, 1988; Chiszar, 1990), an activity continued in captivity (Chiszar et al., 1985).

The eyes of the brown tree snake are large and the pupils are slit-like. A vomeronasal organ is present, but like other colubrid snakes, the brown tree snake lacks anatomically distinct thermosensitive facial pits. Eyes, chemosensory receptors (olfactory epithelium,

vomeronasal organ), and thermosensitive pits are known to be important in the predatory behavior of certain venomous snakes (de Cock Buning, 1983). When denied visual information, pit vipers can still successfully strike prey, presumably by compensating with thermosensitive receptors (Noble and Schmidt, 1937; Dullemeijer, 1961). However, without such alternative sensory receptors the brown tree snake would seem to require alternative sensory input to compensate for loss of visual information during nocturnal forays for food.

To assess feeding performance in the absence of visual information, prey capture success of brown tree snakes with and without blindfolds was compared. The purposes of this experiment were to describe the changes in predatory behavior (normal and blindfolded), and to produce hypotheses about how the sensory versatility of the nervous system might modulate the strike based upon alternative routes of sensory input.

All brown tree snakes used were collected on Guam. All fed readily on mice within one day of arrival, and averaged about two live mice (20 g) per week on an irregular schedule. These snakes (N = 6) ranged from 95 to 122 cm SVL, and were kept individually in glass terraria measuring 50 × 26 × 30 cm. Snakes were housed in a room kept warm year around (22-30 C) and maintained on 12:12 light/dark cycle. Several hours to several days prior to experimental trials, the snakes were moved to an isolated room maintained on similar temperature and light schedules with access limited to authorized personnel (four persons) familiar with the experiments and safety procedures (Gans and Taub, 1964). A clear plexiglass top replaced the screen top used previously. A pair of circular holes (6 cm diameter) were cut at opposite ends of the plexiglass and closed with black rubber stoppers. To conceal the subsequent approach or movement of experimenters, the sides of the glass cages were covered with thick layers of newspaper.

Feeding trials consisted of introduction by the experimenter of a live, preweighed mouse (Swiss-Webster), within a 9.8-26.3 g range, by lifting one of the stoppers, usually the one farthest from where the snake had taken up residence within the cage, and dropping the mouse to the floor of the cage. The hole was closed and the experimenter quickly left the room and recorded (and observed) subsequent events on an external video monitor connected to a video camera positioned above the cage. Several variables were subsequently scored, including the site struck on the mouse, whether the mouse was held or released, time to death (time from strike to last movement by the prey), time from prey introduction to snake's strike, and range of strike (distance from snake's snout to closest part of the mouse when the strike was initiated); see Kardong (1986) for detailed discussion of each variable. The number of constricting body loops (sensu Greene and Burghardt, 1978) completely wrapped around the prey by the snake was also recorded.

Feeding trials were performed no more frequently than every three days. On a random schedule, each individual snake was temporarily blindfolded and run similarly in a feeding trial. The blindfold consisted of a small square of black, opaque electrical insulating tape. A snake to be blindfolded was hand

TABLE 1. Comparisons of strike behavior in normal and blindfolded *Boiga irregularis*. Site refers to the location of strikes on prey, scored as 1 (head/shoulders), 2 (midbody), or 3 (rump).

	Treatment	N	Mean	SD	P
Strike time	Control	25	30.9 s	77.3	<0.001
	Blind	22	114.0 s	107.7	
Range	Control	25	2.8 cm	3.6	<0.02
	Blind	22	0.9 cm	0.7	
Death rate	Control	25	206.9 s	273.2	NS
	Blind	22	457.9 s	1330.6	
Site	Control	25	1.8	1.3	NS
	Blind	22	2.0	1.4	

captured and restrained while a dab of petroleum jelly was touched to the spectacle of each eye (to make subsequent removal of tape easier); a piece of tape was then carefully placed across each eye. The snake was returned to its cage within 2 min and allowed to acclimate (at least 2 h) before feeding trials began. If a snake struck and swallowed the prey or 10 min passed without a strike, the trial was ended. At the end of each feeding trial, the snake was again hand captured, and the blindfold was inspected to ensure that it had not been prematurely dislodged, then it was removed. All tests for statistical significance used analysis of variance (ANOVA) performed on the SAS (GLM) package of tests (Helwig and Council, 1979).

In 79% (37/47) of the strikes, one or more coils were wrapped around the body of the mouse. Placement of coils was irregular. On occasion, the snake used anterior, horizontal coiling; at other times coils were vertical (sensu Greene and Burghardt, 1978). The anterior, midbody, or even tail might produce the constricting coils about the prey. There was no significant difference in rate of death with increase (or decrease) in coil number. In 50 feeding trials, 25 were controls (no blindfold) and 25 were of blindfolded snakes. Snakes struck at the prey most of the time in both cases (25/25 control; 22/25 blindfolded). Strikes were characterized by a firm grip of the jaws on the prey accompanied by constriction. Comparing control and blindfolded trials, the strike was equally likely to be delivered to any part of the mouse's body— anterior (head/thorax), middle (between pectoral and pelvic girdles), or posterior (rump)—with no tendency to strike one of these three regions more frequently. There were no significant differences in the death rates of mice (Table 1). Blindfolded snakes were no more likely to strike and miss than were controls. However, blindfolded snakes took over three times as long to initiate a strike (\bar{x} = 114.0 s) than did controls (\bar{x} = 30.9 s). Further, normal snakes launched their strike almost three times farther from the mouse (\bar{x} = 2.8 cm) than when blindfolded (\bar{x} = 0.9 cm).

Unlike some venomous snakes (Kardong, 1986), these *Boiga irregularis* did not tend to target the strike predominantly to one particular region of the prey. Brown tree snakes respond vigorously to visual cues (Chiszar et al., 1988a), but chemical cues are also im-

portant in foraging behavior (Chiszar et al., 1988b). Our results suggest that successful predation (striking, constricting, swallowing) can occur in the absence of visual cues. The strike behavior of blindfolded snakes is essentially indistinguishable from normal strikes except that the onset of the strike is delayed and the strike is initiated from a point much closer to the prey by blindfolded snakes. Blindfolding made no difference in the length of time it took to kill the mice once the strike occurred. *Boiga irregularis* lacks any anatomically discrete recessed facial pits involved in thermoreception. Thus, such a sense organ is not involved in compensating for the absence of visual cues when blindfolded. However, diffusely distributed intraoral receptors that respond to heat stimuli are known in rattlesnakes (Dickman et al., 1987). If present in *Boiga*, such intraoral thermoreceptors might be the basis for strike compensations when blindfolded.

Alternatively or additionally, vibrations emanating from prey detected via mechanoreceptors (Proske, 1969) might assist localization. Auditory and/or chemical cues could also be involved, but our results cannot discriminate among such possibilities. Our results do indicate that *Boiga* can and does strike in the absence of visual cues as might occur while hunting on dark nights or in dim recesses. This behavioral compensation is probably not based upon switching to the same alternative sensory organs as used by pit vipers. Thus, sensory compensation in *Boiga* probably depends upon a different mix or different emphasis of alternative sensory organs than in pit vipers. If this should prove to be true, then perhaps colubrids (e.g., *Boiga*) and viperids (e.g., rattlesnakes) represent independent but parallel occasions for the evolution of nervous systems that address common problems of switching between sensory modalities when foraging under different conditions (diurnal vs. nocturnal).

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Anuran Phonotaxis Experiments: Does the Speaker Affect Accuracy?

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Studies of phonotactic accuracy in many anurans have shown that the auditory system can guide a female to a sonic target with extreme accuracy (Feng et al., 1976; Gerhardt and Rheinlaender, 1980; Pass-

more et al., 1984). Although an acoustic cue by itself is sufficient to allow for accurate localization, the experimental procedures employed in the measurement of phonotactic accuracy in the past have ignored several factors present under natural conditions. For example, the presence of a visible speaker in an otherwise barren arena may affect localization accuracy of females. Similarly, if a female is close to a sound source, acoustic near-field effects may act as tactile cues.

Hyperolius marmoratus is a small anuran with an interaural distance of approximately 8 mm. Female behavior in phonotaxis experiments and in the field suggests the extensive involvement of vision in the localization of mates (Passmore et al., 1984). We investigated the possible effect of the loudspeaker as a visual cue in aiding localization by using two-dimensional phonotaxis experiments in which approach accuracy was measured when the speaker was visible and when it was concealed from the approaching female. Female accuracy was also measured at different stages of the approach: over the first meter of the approach from the release point; over the last 0.5 m of the approach; and in the final 4 jumps made by the female).

The testing arena consisted of a black cloth floor on which stood a metal frame 2 × 2 m. The frame was raised 15 cm off the ground by six supporting metal legs. A 2 × 2 m piece of tulle was stretched tautly over the frame and attached on all sides. A 5 cm numbered grid was drawn onto the tulle. A 60 W red light bulb was suspended 2 m above ground level in the center of the arena. Females were released 1.5 m from the sound source, on the top of the tulle surface.

Tulle is a light fabric (31 g/m²) which has 32.2 mm diameter perforations per cm. In order to examine the effect of the fabric on sound propagation, 28 sound pressure level readings of the stimulus used in the experiment (see below) were made using a Brüel and Kjaer 2209 impulse precision sound level meter. Measurements were made at corresponding points above and below the arena when the speaker was (a) above and (b) below. A Wilcoxon matched-pair signed rank test revealed that there was no significant difference in the sound pressure level below and above the arena ($T = 29.5$; $N = 12$; $P < 0.05$). The mean difference in the two sets of measurements was 0.6 dB (range = -1 to +1; maximum difference = 1 dB). It can be concluded that the tulle did not obstruct sound propagation. The sound pressure level field of the loudspeaker was examined for heterogeneity and found to be symmetrical and uniform with no conspicuous nulls in the 270° in front of the speaker face.

Calls were broadcast using a Nagra III tape recorder, a Klein and Hummel SB280 140W amplifier, and a Phillips AD50600 12.7 cm diameter loudspeaker. The synthetic acoustic stimulus used covered the normal frequency sweep of the species (2650-3150 Hz, center frequency 2900 Hz). It had a normal repetition rate (1.0 call/s) and was played back at 104 dB peak at 50 cm (the normal sound pressure level of *H. marmoratus* calls).

Amplexing pairs were collected from shallow coastal pans near Mtunzini, Zululand (28°51'S, 31°46'E) during January, 1987. The pairs were transported 6