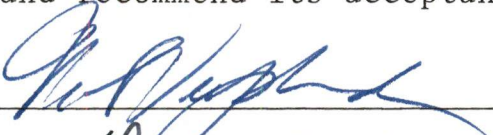
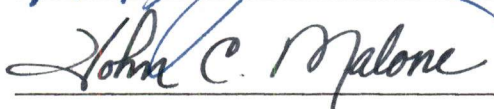


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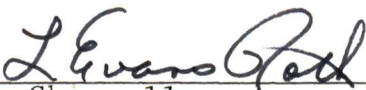
I am submitting herewith a thesis written by Dallas Denny entitled "The Role of Movement in Orientation to and Selection of Prey in the Garter Snake, Thamnophis sirtalis." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Arts, with a major in Psychology.


Gordon M. Burghardt, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:


Vice Chancellor
Graduate Studies and Research

THE ROLE OF MOVEMENT IN ORIENTATION TO AND SELECTION
OF PREY IN THE GARTER SNAKE,
THAMNOPHIS SIRTALIS

A Thesis
Presented for the
Master of Arts
Degree
The University of Tennessee, Knoxville

Dallas Denny
March, 1979

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ABSTRACT

The role of prey movement in the feeding behavior of garter snakes (Thamnophis sirtalis) was investigated in several experiments. Twelve snakes were repeatedly presented with paired (nonmoving and rotating) sections of earthworm (Lumbricus terrestris). Additionally, intensity of odor of earthworm was varied (assuming intensity of earthworm odor increases with mass), and the performance of a tongueless snake compared to controls.

Preliminary tests indicated that garter snakes will select (by open-mouthed attack) rotating over nonmoving sections of earthworm across a wide range of speeds, with an optimum between 16 and 64 revs/minute (as measured by frequency of and latency to attack). However, it was possible that chemical or vibratory cues from the rotating sections were attracting the snakes in some way. Experiment 1 demonstrated that both blocking the odor from the sections and presentation of speeds greater than 500 revs/minute decreased response to moving sections; a second experiment showed that at 22-32 revs/minute moving sections were selected (as measured by approach) over nonmoving sections when odor from both was blocked, and that the snakes exhibited no preference under these conditions when visual cues were blocked.

Experiment 3 assessed the effects of varying odor conditions upon selection of moving and stationary prey, when a new section of the cage, complete with moving or nonmoving plastic earthworms, was made available to the snakes. Strong earthworm odor resulted in a sustained high rate of tongue-flicking while, with no odor present, snakes initially showed a high rate of tongue-flicking, but returned to baseline within several minutes.

Experiments 4 and 5 studied the effects of tongue removal upon the selection of moving and nonmoving prey. Gross changes in the feeding sequence were noted. A tongueless adult fed by opening its mouth and thrashing about its cage when presented with earthworm odor; a control showed the normal stalk-and-strike sequence. The tongueless snake showed a weaker attraction to the moving earthworm than did the controls.

Ordinarily, tongue contact with prey seems to precede attack. However, when presented with rapidly moving sections of earthworm (over 100 revs/minute or its linear equivalent), snakes probably do not touch the sections with their tongues before striking. The omission of a phase of the stalk-and-strike sequence may enable the garter snake to capture rapidly-moving quarry which might otherwise escape.

Selective attention to visual cues, in this instance, might lead to less dependence upon chemical cues. Several

instances of snakes attending to one sensory modality while "ignoring" another are discussed.

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CHAPTER I

INTRODUCTION

A number of accounts indicate the importance of movement, and especially odor, of prey in the feeding of snakes (reviewed by Burghardt, 1970). Chemical cues have been shown to be essential for feeding in neonate natricine snakes and sufficient for recognition and location of prey in a number of species (Burghardt, 1970). However, studies of visual cues have rarely been conducted in the absence of odor from the prey tested (some exceptions are Burghardt, 1966; Drummond, in press; and Wiedemann, 1931). Herzog and Burghardt (1974) note that chemical cues "stirred up" by prey may have an effect that has been attributed to movement.

Previous studies have not used prey whose movement is under strict control of the experimenter. Movement of living prey is intermittent and variable. Furthermore, different portions of the prey often move at different rates (Dieffenbach and Emslie, 1971). Irregularity or sporadicity of movement may be important in the feeding of a number of predators (Robinson, 1969), and other visual cues such as contrast of prey with background (Czaplicki and Porter, 1974; Porter and Czaplicki, 1977) and size of prey (Burghardt, personal communication) are of importance

in the feeding of natricine snakes. The present experiments concentrate upon the effects of continuous movement at various speeds. The type of movement used was rotation of prey in a horizontal plane.

When odor of prey is present, movement seems to hasten and direct attack in a number of species of snakes. Gettkandt (1931) and Wiedemann (1931, 1932) found that movement of prey attracts the European grass snake (Natrix natrix), and Kahmann (1932) found that blinded N. natrix were less efficient than normal animals in locating food. MacDonald (1973), in a rare attempt to quantify movement of prey, presented boa constrictors (Boa constrictor) with mice which exhibited different levels of activity. Mice which were "active" (i.e. alert and attempting to move about) were attacked more quickly than dead or anesthetized mice. Similarly, Herzog and Burghardt (1974) showed that Western yellow-bellied racers (Coluber constrictor mormon) located and attacked live crickets (Acheta domestica) much more rapidly than dead crickets. Dieffenback and Emslie (1971) found that Japanese rat snakes (Elaphe climacophora) most often strike mice on or near the head; they noted that the head of the mouse moves more than the rest of the body and that their snakes oriented towards the head before striking. Burghardt (1966) found that garter snakes showed increased rates of tongue-flicking and oriented towards a sealed vial containing living prey. These snakes

consistently oriented towards the part of the vial with the most activity. Finally, Dullemeijer (1961), as well as Chiszar and his co-workers (Chiszar and Radcliffe, 1976; Chiszar, Scudder and Knight, 1976; Chiszar, Radcliffe, and Scudder, in press) found that rattlesnakes respond primarily to visual and thermal cues before they strike their prey.

Curio (1976, p. 89) has suggested that "short-term shifts of attention" occur in predators, perhaps due to "continuing prey excitation." Evidence Curio cites in support of this are findings by Messenger (1968) that cuttlefish (Sepia officinalis), which will not ordinarily attack dead prawns, will attack a prawn which has already been attacked and paralyzed if the prawn is reintroduced, and by Herzog and Burghardt (1974), who found that juvenile racers showed different sequences of attack to live and dead crickets. The snakes oriented towards live crickets as soon as movement occurred, and then pursued the crickets around the cage, striking and often missing. Dead crickets elicited no such orientation. Instead, snakes would typically begin searching movements, tongue-flicking at the substrate. Although the snakes were quite capable of locating the dead crickets in the absence of movement, they would begin random searching movements if a cricket stopped moving, as if they had lost visual orientation. Even when the snake's head was quite close to the cricket (1-2 cm),

the snakes were often unable to make a successful attack. Kahmann (1932, 1934) and Smith and Watson (1972) had similar findings, using the European grass snake (N. natrix) and the corn snake (Elaphe guttata), respectively.

A number of other studies also seem to support Curio's suggestion. Roth (1976), working with the Italian bolito-glossine salamander Hydromantes italicus, concluded that this species, which lives at various times of the year inside and outside of limestone caves, has two guidance systems for prey-catching behavior, a visually guided system and a system guided by chemical cues. In total darkness H. italicus can detect and locate prey, but in the light is often unable to find prey when there is little contrast with background. The water snakes Natrix s. sipedon and N. r. rhombifera also have trouble locating prey which do not contrast with background (Czaplicki and Porter, 1974), although these snakes can learn to capture prey that do not contrast with the background (Porter and Czaplicki, 1977).

Another example of a "short-term shift of attention" occurs in rattlesnakes (Dullemeijer, 1961; Chiszar and Radcliffe, 1976; Chiszar, Scudder, and Knight, 1976; Chiszar, Radcliffe, and Scudder, in press). These snakes depend heavily upon thermal and visual cues until the prey is bitten, and then locate their prey by chemo-sensory means. Unbitten prey is usually ignored while

the snakes search for their poisoned prey. Chiszar and his co-workers account for the reliance on different sensory cues during the different phases of the feeding sequence of rattlesnakes as a "switching on and off" of various processes, with, for instance, the strike "switching off" reliance upon visual and thermal cues and "switching on" the chemical senses. Earlier Naulleau (1964, 1966) divided the feeding of vipers into two phases, the first of which was controlled almost totally by visual stimuli, and the latter by chemical cues.

Tinbergen (1951) has stressed the distinction between releasing and directing functions of stimuli. Releasing and directing stimuli may be spatially separated and may act through different sensory modalities. An example from Tinbergen (1951) illustrates this point nicely:

Daphnia, swimming in water with a high carbon dioxide concentration, gather near the surface. The function is obvious: in polluted water, the surface layer, being in contact with the air, is relatively rich in oxygen. Analysis shows that two stimuli play a part in this reaction: chemical stimulation by the carbon dioxide, and a visual stimulus. In a glass jar lighted from underneath Daphnia will swim downwards as soon as CO₂ is added. The carbon dioxide merely releases the response, which is directed by the light.

--p. 82

Are different stimuli responsible for releasing and directing different parts of the feeding sequences of garter snakes? Does reliance upon one modality cause the snake to show no response to other modalities, and can this be the cause of the "short-term shift of attention" noted by

Curio (1976)? In order to answer these questions and to study the effects of visually perceived movement and the extent of interaction between moving visual and airborne chemical cues in the selection of prey by snakes, I systematically varied the rate of movement of real and imitation items of prey. Garter snakes (Thamnophis sirtalis) were allowed a choice between rotating and stationary prey in a test chamber which was at various times free from or impregnated with the odor of prey. Chemical and visual cues were presented from the same and different locations in space.

CHAPTER II

GENERAL METHODS

Subjects

Twelve common garter snakes (Thamnophis sirtalis sirtalis), two Chicagoland garter snakes (T. s. semi-fasciata), and two red-spotted garter snakes (T. s. concinnus) were tested. Snout-vent lengths ranged from 24 to 75 cm. All snakes were fed on diets of earthworms (Lumbricus terrestris) or earthworms and goldfish (Carassius auratus). Subjects were deprived of food for at least five days before they were tested.

Testing Environment

At least four days prior to testing snakes were individually housed in covered 60 x 30 x 30 cm high wood and Plexiglas^R cages. The snakes lived in a 50 x 30 x 30 cm section of the cages. A water dish, small rock, and plastic shelter were provided in this home chamber. An opaque Plexiglas^R divider separated the snakes from a 10 x 30 x 30 cm testchamber (Figure 1). During each test the divider was removed, giving the snakes access to the test stimuli. Absorbent paper (Kimpack^R standard cage liners) covered the bottom of the home chamber. The floor of the testing chamber was covered with a strip of newspaper.

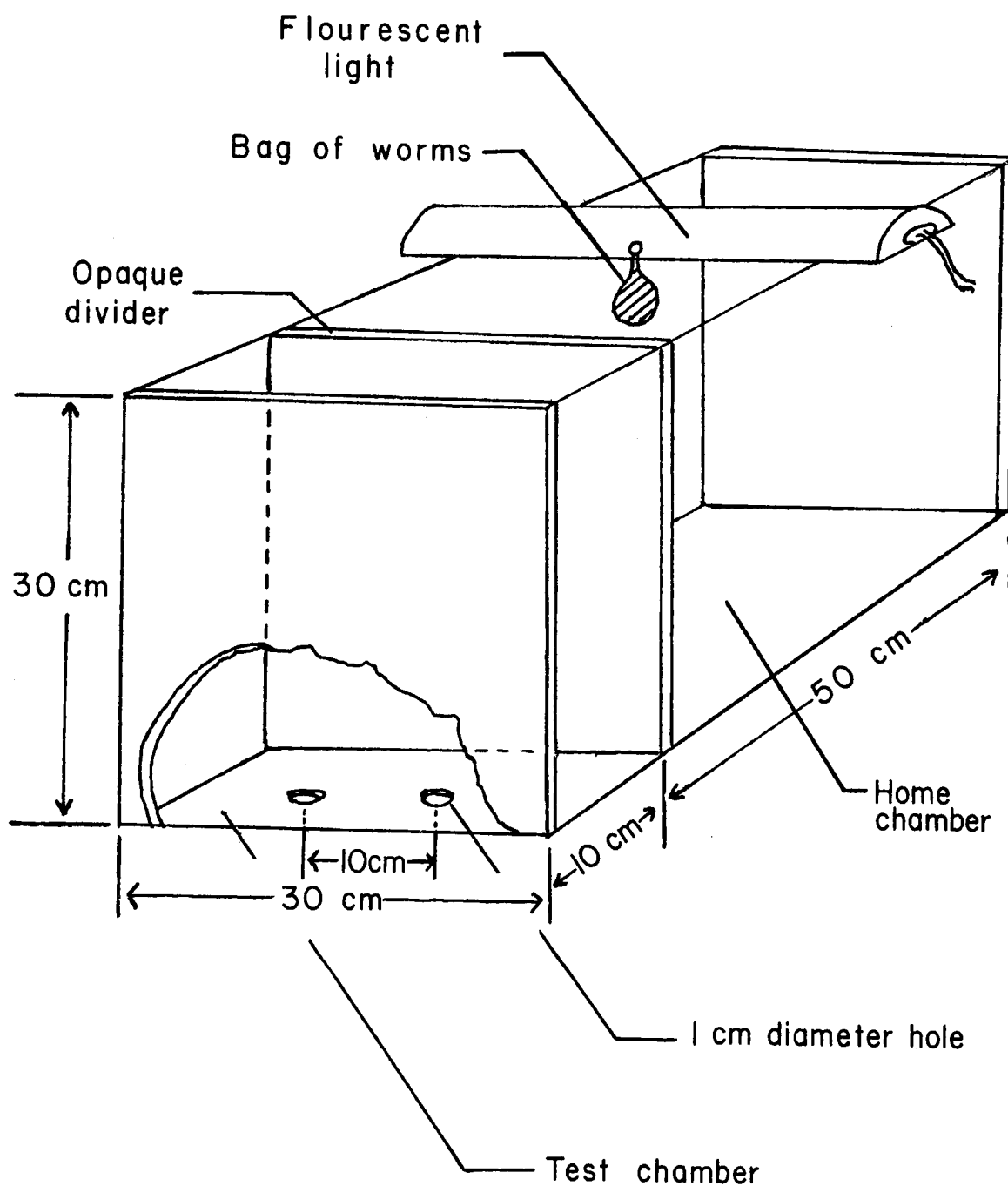


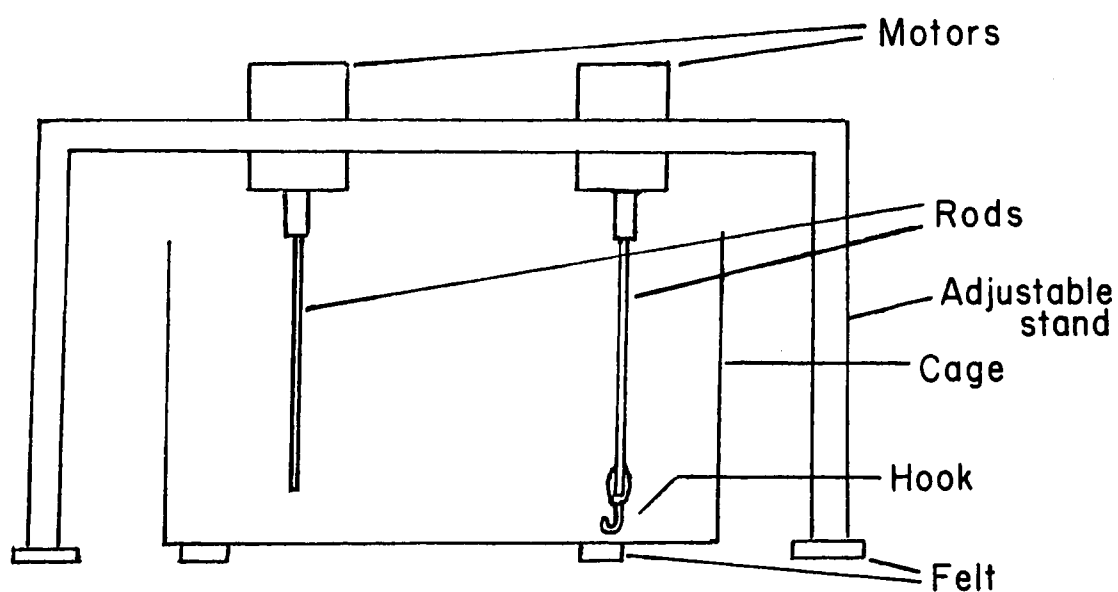
Figure 1. Home and testing chamber.

Temperature in the experimental room ranged between 22° and 26° C. A 12:12 hour light/dark cycle was maintained until the summer months; as the days grew longer, natural lighting was substituted for fluorescent lighting. All testing took place during daylight hours between 24 June and 29 July, 1975, and 29 June and 5 July, 1977.

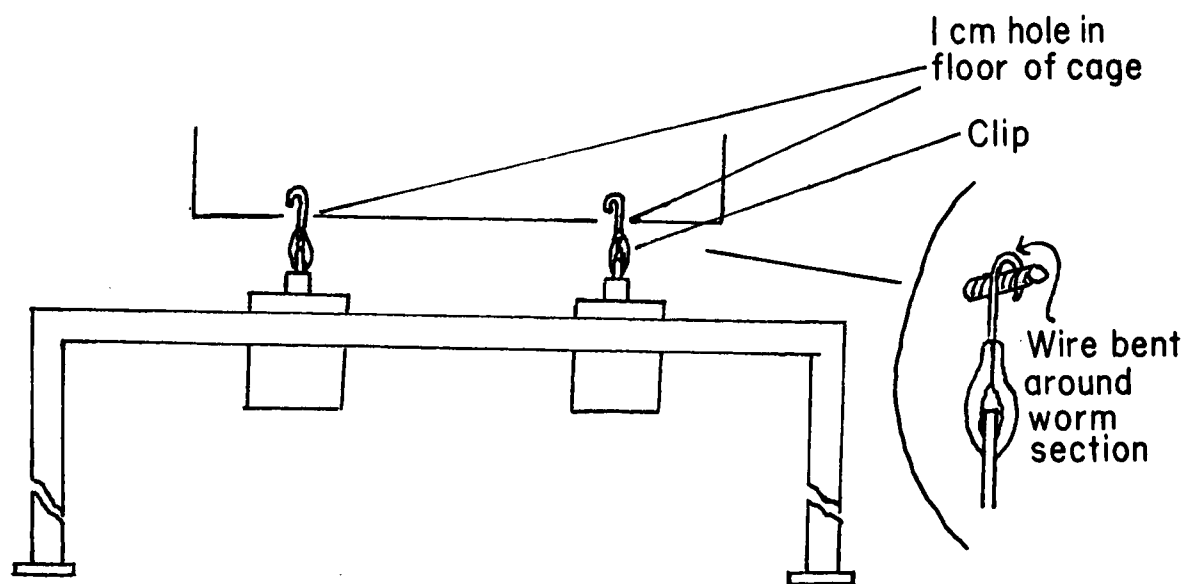
Materials and Procedure

Two reversible, remotely controlled Minarec^R electric motors were used to vary the speed of rotation of 1.5 cm sections of earthworm (Lumbricus terrestris). Earthworm (nightcrawler) sections were fastened onto hooks which were secured to the armatures of the motors (Figure 2, inset). Pieces of worm were introduced from below, through holes in the floor of the cages (Figure 2). The sections of worm were spaced 10 cm from each other and centered in the test chamber 1 cm above the floor. The side on which the moving section was presented varied from left to right according to a random sequence (Fellows, 1967), to avoid confounding by a tendency to attack to the left or right.

By turning on one or both motors, pieces of worm could be rotated at various speeds. Table 1 gives the linear speed of the ends of the earthworm sections for each speed used. Although the sections of earthworm were rotating in a horizontal plane, from the snake's usual perspective (a point near the floor of the cage), the movement appeared as a shortening and lengthening of the worm sections, at a



A. TOP PLACEMENT



B. BOTTOM PLACEMENT

Figure 2. The apparatus, illustrating placement of worm sections.

TABLE 1
ABSOLUTE AND RELATIVE MOTION OF WORM SECTIONS

Linear speed of ends		Apparent change in length when viewed from the same hori- zontal plane
<u>Revs/min</u>	<u>Cm/sec</u>	<u>Cm/sec</u>
1	0.08	0.08
16	1.26	1.28
22	1.73	1.76
32	2.51	2.56
256	20.10	20.48
512	40.21	40.96
1024	80.43	81.96
2048	160.85	163.84

rate twice that of the speed of rotation. That is, at 32 revs/minute, a section would appear to alternately shorten to approximately .3 cm (its thickness) and grow to 1.5 cm (its length) 64 times per minute. This apparent movement is not totally un-wormlike (earthworms do lengthen and shorten their bodies), although some speeds presented greatly exceeded wormlike speeds. At times snakes did elevate their heads enough so that the circular motion of the prey could be detected. However, their heads were generally kept close to the ground. Also, the distance traversed by the ends of the worm sections in their circular course was approximately equal to the apparent increase and decrease of the sections when viewed from a horizontal perspective (Table 1). Therefore, speed of movement was taken to be equivalent from both perspectives.

Maximum length of the moving section of worm was the same as the length of the nonmoving section when viewed from the testing chamber. From the extreme rear of the testing chamber, a distance of 55 cm from the worm sections, the angles subtended by the moving worm sections were 1.56° maximum and $.31^{\circ}$ minimum; from the border of the testing chamber, 5 cm from the sections, the angles were 17.06° and 3.42° , respectively, and from a distance of 1.5 cm from the sections (attack usually occurred after a pause from a similar distance), 53.13° and 11.42° .

Before sectioning, earthworms were killed by scalding for 30 seconds in hot water (otherwise sectioned worms moved on the hooks of their own accord). The end and clitellum sections were discarded. Sections were kept moist until use by placing a damp towel over them. When positioning worm pieces, care was taken not to touch them against any part of the test chamber. Hooks were washed thoroughly before and after each trial, and the newspaper covering the floor of the test chamber changed between trials. Test chambers were washed with soap and water before testing began and after testing was ended on each day trials were run.

To provide airborne prey odor, a porous cloth sack (a laundered sock) was filled with six or seven earthworms. This "wormbag" was fastened and hung over the center of the home chamber during testing.

During testing, the cage top, water dish, and rock were removed and the cages transferred to a testing table. A wooden partition equipped with a one-way mirror placed on one end of this table separated the subjects from the experimenters. Two 15 watt cool-white fluorescent lights placed on the snakes' side of the mirror provided illumination. Room lights were turned off during testing. To reduce vibrations, felt strips were placed under the table, under the cages, and under the stand that held the motors.

After an habituation period which varied in different experiments from 4 minutes to 30 seconds (long habituation

periods were found to be generally unnecessary as methods were refined), the divider was removed by hand, allowing the snakes access to the test chamber and a view of the worm sections. Although behavior was recorded throughout each trial, the primary measures noted were orientation to either worm section (characterized by freezing with the head pointed towards a worm section), the time the snake's head entered the test chamber, latency to attack (from divider removal), and worm section chosen (moving versus nonmoving and left versus right). These observations were verbally recorded on a cassette tape recorder; immediately after each trial the tape was replayed and the data transcribed.

The motors were turned off immediately upon attack to either worm section; the snakes were allowed to remove and eat the piece of worm attacked. When necessary (after approximately 10 percent of attacks), the experimenters intervened and assisted a snake by removing the worm section from its hook.

In the first experiment three or four trials were run per day for each snake. In later experiments more trials were run, to a maximum of twenty per day for each snake. In all experiments trials were terminated at a preset time (usually 5 minutes) if no open-mouthed attack occurred. Trials were also terminated if a snake crawled completely under the paper lining in its home chamber.

CHAPTER III

EFFECTS OF ODOR AND MOVEMENT FROM DIFFERENT LOCATIONS IN SPACE

A. Introduction

After live prey is introduced, garter snakes ordinarily begin crawling about their enclosure flicking their tongues vigorously. The snakes sometimes orient towards the prey, but may approach without apparently orienting. When a snake has reached a distance of approximately 2-4 cm from its prey, it hesitates briefly; sometimes the tongue, as it flicks in and out, can be seen to touch the prey. During the hesitation the snake often follows movement of the prey with its head, and may inch slowly forwards.¹ A sudden movement by the prey or by the experimenter can cause retreat at this point. The prey is next struck quickly with an open-mouthed attack, and ingestion begins.

Results of a number of preliminary tests using paired moving and stationary prey indicated that movement can hasten and direct attack, in the presence of chemical cues.

¹Roth (1976) found a similar pause in the Italian bolitoglossine salamander, Hydromantes italicus. Roth simulated moving prey by using disks of black cardboard and moving his stimuli in a stepwise manner as well as in a continuous manner.

Snakes generally followed the above sequence, with one exception--when moving prey were rotating very rapidly (128 and 256 revs/minute), attacks sometimes occurred with very short latencies (3-15 seconds). In this case the snakes would orient to the moving section of worm as soon as the divider was removed, or very shortly thereafter, when the head was turned in the general direction of the worm sections. Almost immediately afterwards, the snake would crawl very rapidly into the test chamber and attack the moving section. Snakes did not pause when near the section, but would seize it without slowing, and would crawl directly over the stationary sections of worm if they were encountered on the way to the moving (this occurred when the snake oriented to the moving section from a spot near the divider). This never occurred at slow speeds of rotation (usually, if one section was encountered on the way to another, it was attacked instead).

The hesitation the snakes usually exhibited before attack may have allowed actual tongue contact with the prey. Such contact of the tongue with prey seems to be essential for elicitation of attack in newborn garter snakes which have never eaten (Sheffield, Law, and Burghardt, 1968). These researchers noticed that at least one tongue-flick made contact before every attack to cotton swabs containing water-based surface extracts of prey. In many cases they could not see the tongue touch the swab, but an electronic

counting device, which registered whenever any part of the snake touched the swab, indicated that contact invariably occurred before attack. These workers concluded that a non-volatile molecule, which was picked up by the tongue on contact, was responsible for the elicitation of attack in their snakes.

With older snakes, however, contact of the tongue with prey is not essential, although it may still occur in most instances. Burghardt and Pruitt (1975) found that juvenile garter snakes recovered to near previous levels of attack after their tongues were removed, although newborn snakes (ingestively naive) would not feed. Burghardt and Pruitt noted that the juveniles did have part of their tongues left (there were still protrusible stubs), and so were reluctant to conclude that the limited feeding experience of these snakes was responsible for the differences observed between them and the naive group. Therefore they selected an adult garter snake and removed its tongue as completely as possible. This snake would attack pieces of nightcrawler when they were presented on a glass plate but not touched to the snout, and ate "readily, although somewhat abnormally" (p. 193) after operation. Burghardt and Pruitt concluded that this snake relied more on visual or olfactory cues than newborn snakes, and noted that the tongue does not seem to be essential for feeding in adult garter snakes. (Gettkandt also had a tongueless snake, a N. natrix, which readily ate.)

I felt that the very rapid attacks I noted may not have allowed time for contact of the prey with the tongue. This could not be determined with any certainty, however, without detailed film analysis. Additionally, it was difficult to tell to what extent chemical cues were implicated in the selection of moving earthworm sections in my preliminary investigations. Was a "stirring up" (Herzog and Burghardt, 1974) of airborne chemical cues important in leading the snakes to the moving earthworm sections? Airflow in the vicinity of the moving pieces of worm was not measured. However, Eisner, Kriston, and Aneshansley (1976) measured airflow near an "overhead twirler" which was smaller than, but shaped identically to, a hook carrying an earthworm section. A 4.1 mm long twirler operating through a range of 75-126 revs/minute was found to cause a periodic (due to its two-bladed nature) airflow of up to 0.5 mm/second at a spot 2 mm outside the circle of rotation. It was decided on the basis of Eisner, et al.'s measurements that the rotating earthworm sections stirred up the air sufficiently to act as a possible cue.

B. Experiment 1

In this experiment a wide range of speeds was tested, first with chemical cues from the prey present, and then with odor from the prey blocked (in both cases airborne odor of prey was introduced from overhead prior to testing).

Methods

Subjects. Three T. s. sirtalis that were familiar with the apparatus and procedures were tested. All three snakes were born and raised in the Reptile Behavior Laboratory at the University of Tennessee at Knoxville.

Procedure. The snakes were allowed choices between nonmoving earthworm sections and sections moving at 1, 16, 32, 256, 512, 1024, and 2048 revs/minute. One snake was given the tests in ascending followed by descending order; the remaining two snakes were given the tests in descending followed by ascending order. The sequences were then repeated with an addition: transparent drinking glasses of approximately 0.25 liter capacity (diameter was 6 cm) were inverted over the test sections.

When glasses were in place open-mouthed attacks generally did not occur, even though the snakes oriented upon and approached the sections of worm. Therefore the worm section selected was considered to be the one whose glass was first touched by the snout or tongue of the snakes, and latency was scored as time from divider removal until one of the glasses was so contacted. For purposes of analysis the slowest three and fastest three speeds were grouped ("slow" and "fast" speeds, respectively).

Results and Discussion

Selection of worm sections. When glasses did not block worm odor, there was a preference for moving sections at "slow" speeds (Table 2). Figure 3, which shows selection of moving sections at each speed, illustrates these effects. The snakes selected moving sections less frequently when glasses were in place than when they were not at each of the seven speeds tested ($p < 0.025$, sign test). However, the shape of the curves is remarkably similar. Selection of moving sections was less frequent at "fast" speeds than at "slow" speeds in each (covered and uncovered) condition ($p < 0.05$, binomial).

Selection following orientation behavior. Orientation from (all locations) outside the test chamber occurred on about half of the trials for each snake. Following orientations to one of the worm sections, moving sections were chosen more frequently than nonmoving at "slow" speeds (sections covered and uncovered) and when sections were uncovered ("slow" plus "fast" speeds) (Table 3). At "fast" speeds nonmoving sections were chosen over moving when no orientation occurred (14 and 5 choices, respectively, $p < 0.05$, binomial).

Latencies for all attacks. Latencies for trials when glasses were present were not compared with latencies for trials without glasses because of the different measures

TABLE 2
 FREQUENCY OF SELECTION OF MOVING AND NONMOVING
 WORM SECTIONS WHEN COVERED AND
 UNCOVERED BY GLASSES
 (EXPERIMENT 1)

	<u>Slow</u>		<u>Fast</u>	
	(1, 16, 32 RPM)		(512, 1024, 2048 RPM)	
	M	NM	M	NM
Not Covered (Open-Mouthed Attack)	15*	1	5	13
Covered (Touched Glass with Snout or Tongue)	9	6	1	10*

* $p < .01$, bionmial test, two-tailed.

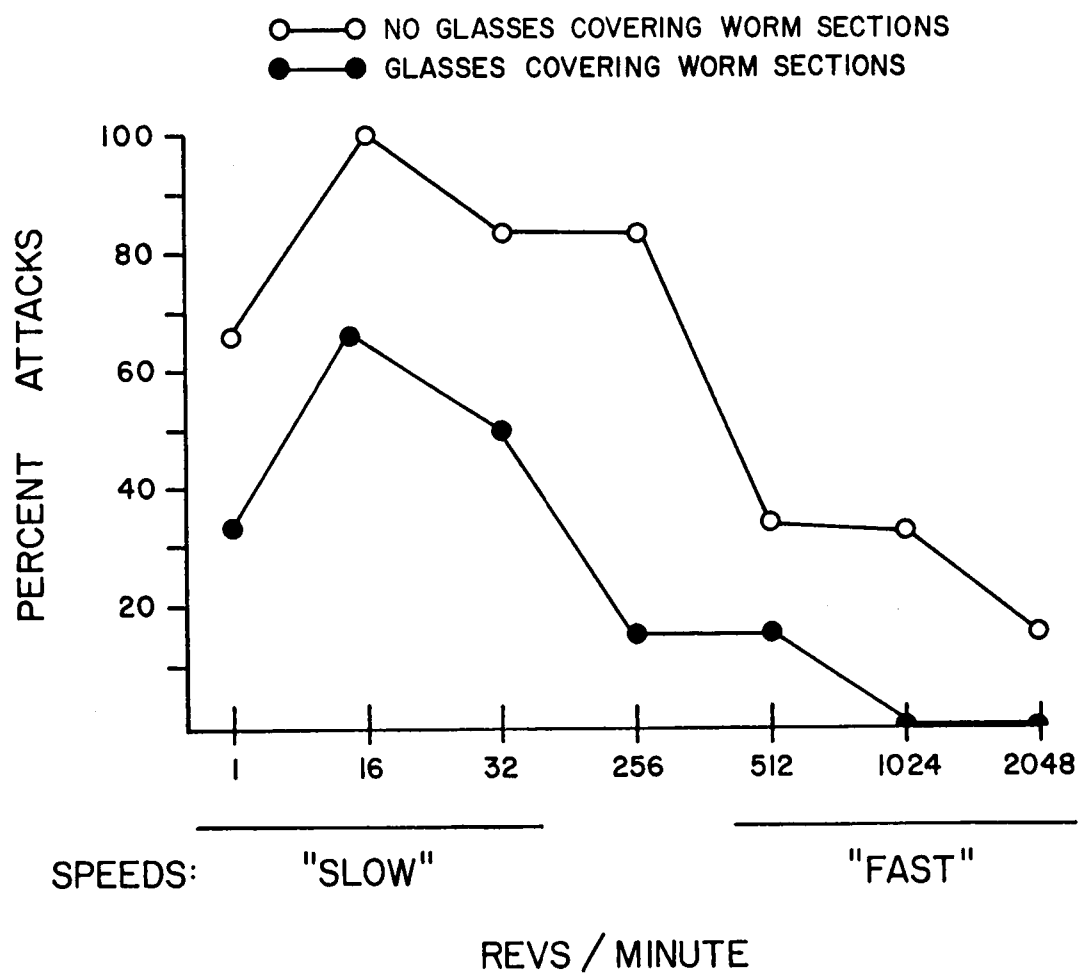


Figure 3. Percent of selection of moving earthworm sections at each speed (Experiment 1).

TABLE 3
SELECTION OF WORM SECTIONS FOLLOWING ORIENTATION
(EXPERIMENT 1)

<u>Worm sections covered plus uncovered</u>	<u>Selected</u>	
	<u>M</u>	<u>NM</u>
"slow"	17**	4
"fast"	2	8
<u>"Slow" plus "fast" speeds</u>		
covered	5	6
uncovered	15*	6

* $p < 0.05$, binomial test, two-tailed.

** $p < 0.01$, binomial test, two-tailed.

of preference used. Instead, latencies were combined and averaged. Figure 4 shows this combined average across speeds. The lowest latencies occurred at 256 revs/minute.

An alternative latency measure, the time from entry into the test chamber until attack or contact with the glass, showed that the snakes spent a longer time in the vicinity of the earthworm sections at "fast" than at "slow" speeds before attack or contact (Figure 4).

Discussion. At 1024 revs/minute and above the pieces of worm were rotating so fast that to the experimenters they did not appear to be moving. The finding that, with glasses in place, the snakes avoided touching the glasses covering the moving sections at "fast" speeds may indicate that movement may have been detected but did not stimulate approach behavior. Occurrence of orientations to moving worm sections at "fast" speeds further suggests that movement was detected.

The lack of preference for moving earthworm sections when glasses were in place may have been due to the wide range of speeds presented, especially considering the small sample size. The 1 and 16 revs/minute speeds were demonstrated in preliminary studies to be not particularly effective in directing attacks, and the 512, 1024, and 2048 revs/minute speeds were demonstrably too fast to direct attack in this experiment.

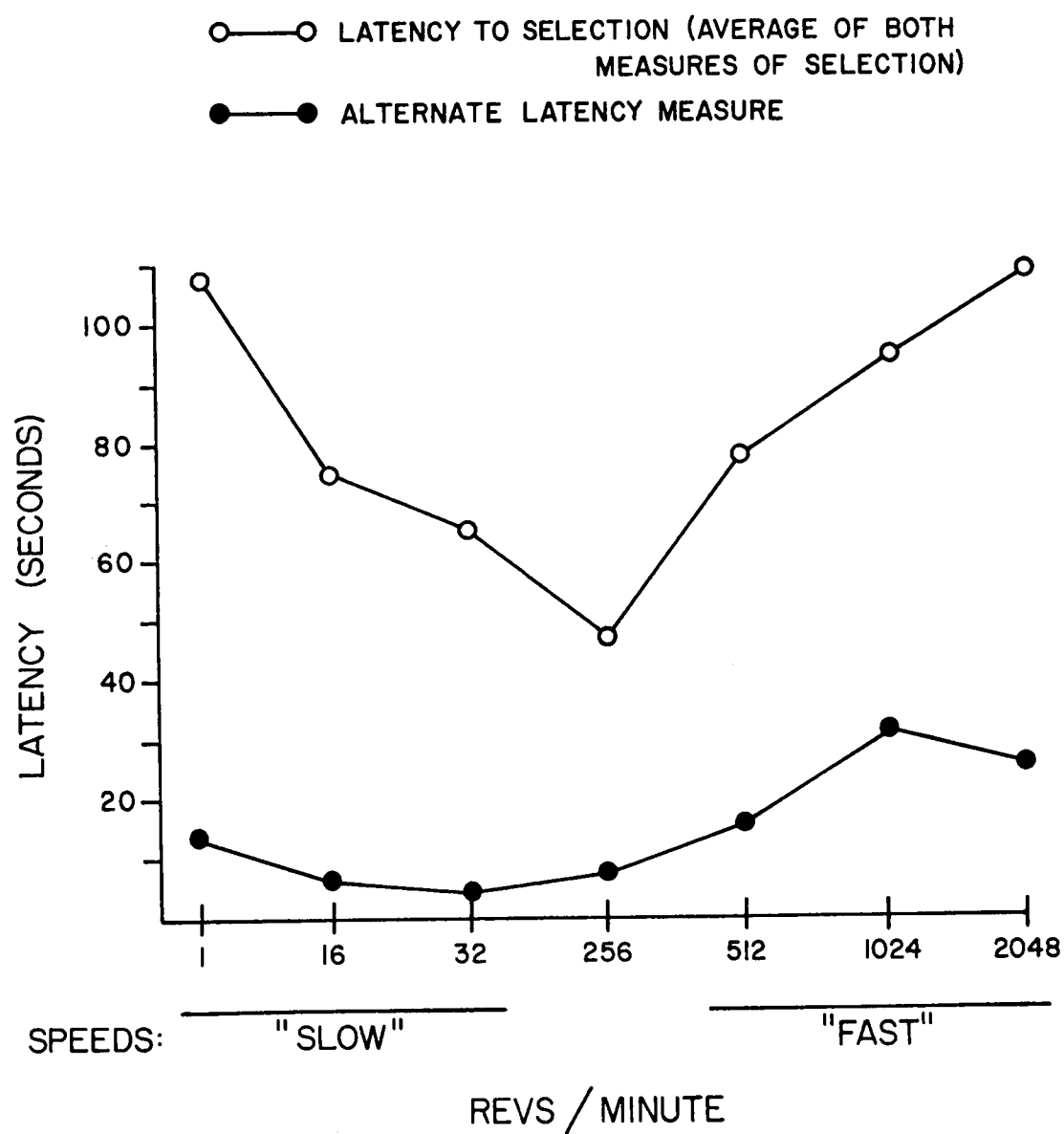


Figure 4. Mean latency to selection and alternate latency measure for combined (glasses plus no glasses) conditions (Experiment 1).

The snakes spent most of the habituation period in the vicinity of the divider, often attempting to climb over it. This occurred when test sections were covered with glasses, so odor from worm sections could not have been a factor; neither could the wormbag have been directing the snakes to the divider (it was suspended over the middle of the food chamber). It seems that the snakes had learned the location of the food, as Loop and Small (1974) found with Tegu lizards (Tupinambis teguixin), which returned to locations where they had been fed even when odor trails led directly to different sections of their cages.

C. Experiment 2

It seemed likely that in the preceding experiment a preference for moving earthworm sections (independently of chemical cues from the sections themselves) could have been masked by the presentation of pieces of worm which were rotating at speeds which were either too fast or too slow to direct attack. This experiment tested for a preference, with odor from test sections both present and eliminated, at speeds which had been demonstrated in preliminary investigations to be effective in directing attack when their odor was not blocked.

Methods

Subjects. Three T. s. sirtalis were used. Two were subjects in the previous experiment, and the remaining

snake (snout-vent length 49 cm) was previously untested. It had been born in the reptile laboratory.

Procedure. The snakes were presented with earthworm sections moving at 22 or 32 revs/minute, paired with non-moving sections. Sections were covered or uncovered (as in Experiment 1, with glasses) in a random fashion (1:1, Fellows, 1967). Each snake was given a maximum of 20 trials daily. Trials were conducted until preference for moving or nonmoving worm sections was demonstrated for either the uncovered or covered condition ($p < 0.025$ binomial). At this point Fellows' sequence was replaced by one which consisted mainly of the condition which had not reached significance (3:1, random). It was not necessary to run more than 28 trials or "little experiments" (see Cole, 1962, for a description of this method) for results to reach the 0.025 level of significance, two-tailed, for preference to moving sections in the glass condition. Selection of covered and uncovered worm sections was scored as in Experiment 1.

Results and Discussion

All three snakes chose the moving pieces of worm more often than the nonmoving pieces when the glasses were in place (Table 4; $p < 0.025$, binomial). Two of the three chose the moving sections more often when glasses were not in place ($p < 0.025$, binomial). Results for the snake

TABLE 4
 FREQUENCY OF SELECTION OF MOVING AND NONMOVING
 WORM SECTIONS (EXPERIMENT 2)

	<u>Snake</u>					
	#22 (22 RPM)		#51b (32 RPM)		#26 (naive) (22 RPM)	
Worm Section:	<u>M</u>	<u>NM</u>	<u>M</u>	<u>NM</u>	<u>M</u>	<u>NM</u>
Condition:						
Glasses	9*	1	7*	0	12*	2
No Glasses	7*	0	7*	0	10	4

* $p < 0.02$, binomial test, two-tailed.

that was tested at 32 revs/minute were significant in the minimum number of trials; that is, this snake never chose the nonmoving section. This could have been caused by individual differences or by the speed presented to this snake, which may have elicited a stronger or more reliable preference than did 22 revs/minute. Latencies were short for all snakes, and did not differ among snakes or for attacks to covered and uncovered worm sections.

The naive animal took longer to achieve significant results than did the two experienced snakes (Table 4). It did not, however, select moving sections more often in later trials than in earlier ones, nor did latencies change greatly as trials progressed.

In both this and the previous experiment several attacks occurred when the glasses covered the earthworm sections. This happened only to the moving sections, however, suggesting, as did the extremely rapid attacks in preliminary investigations, that movement sometimes causes attack without prior tongue contact with the prey (in the presence of prey odor).

CHAPTER IV

EFFECTS OF MOVEMENT UNDER VARYING ODOR

CONDITIONS: EXPERIMENT 3

In the previous experiments no attempt was made to test for reactions to moving worm sections in a situation completely free from odor of prey. The snakes were exposed to odor from a suspended source even when test sections were covered. In this experiment snakes were tested both in the absence of prey odor and with odor present. This enabled me to determine whether, for ingestively experienced garter snakes, movement of prey is sufficient to elicit attack. Will older snakes, unlike neonates, show open-mouthed attack to moving prey when there is no odor of prey? Does experience or maturation lead to increased reliance on visual cues? Also, will mere closeness to prey, in the presence of chemical cues, but without cues from the prey itself, elicit attack?

Methods

Subjects. Four adult snakes, two T. S. sirtalis collected in East Tennessee during May and July, 1975, and two T. s. semifasciata collected in Cook County, Illinois and received in July, 1975, were tested. Snout-vent lengths ranged from 38 to 65 cm. All four snakes were naive to our experimental situation.

Procedure. The snakes were given two series of seven trials. Half were first tested with a wormbag in place. The remaining half were first tested with a control bag free of prey odor. Conditions were reversed for the second series of seven trials. For the first two trials in each series 1.5 cm sections of unscented plastic earthworms were presented. The usual 1.5 cm sections of Lumbricus were presented for the remaining trials.

As a general measure of activity, tongue-flicks were counted during each minute of the first two trials in each series. Each time the tongue was extended, oscillated up and down, and retracted was counted as one tongue-flick; this corresponds to what Ulinski (1972) called a "tongue-flick cluster."

Each trial was divided into four periods: a three minute baseline, with no wormbag or control bag present and with the divider in place; a three minute habituation, with wormbag or control bag in place but the divider still down, a four minute period with the divider raised but both motors off (period A); and a four minute period with both motors rotating at 32 revs/minute (period B). Trials were terminated upon completion of period B when the plastic nightcrawler was used. When the real earthworm sections were used trials were terminated upon attack to one of the worm sections.

Results and Discussion

Rate of tongue-flicking (trials with plastic earthworm only. Tongue-flicks/minute increased when the wormbag was added ($p < 0.01$, t-test; Figure 5). There was no corresponding increase when the control bag was added. When the motors were turned on (period B), there was no difference in tongue-flick rates for the first two minutes, but in the last two minutes of period B the rate of tongue-flicking by the wormbag group remained constant, while the rate of tongue-flicking by the control bag group decreased ($p < 0.05$, t-test for minutes 3 and 4, not significant for minute 1 or minute 2).

Attacks. The last five of each series of seven trials resulted in attack, usually before period B began. Several open-mouthed attacks occurred to plastic worm sections during period B; in one instance the control bag was in place--worm odor had not been introduced into the cage. While precautions were taken to keep odor of earthworm out of the testing room during this condition, there is a possibility that some contamination occurred. This attack happened on the second series of trials, after the snake had attacked and eaten a number of earthworm sections in the test chamber; therefore, learning cannot be ruled out as a cause of the attack. However, although orientation and approach to sections of earthworm frequently occurred

PERIOD: BASELINE (DIVIDER IN PLACE, NO WORMBAG)
 HABITUATION (DIVIDER IN PLACE, WORMBAG OR
 CONTROL ADDED)
 A (DIVIDER REMOVED, MOTORS OFF)
 B (DIVIDER STILL REMOVED, BOTH MOTORS ON
 AT 32 REVS/MINUTE)

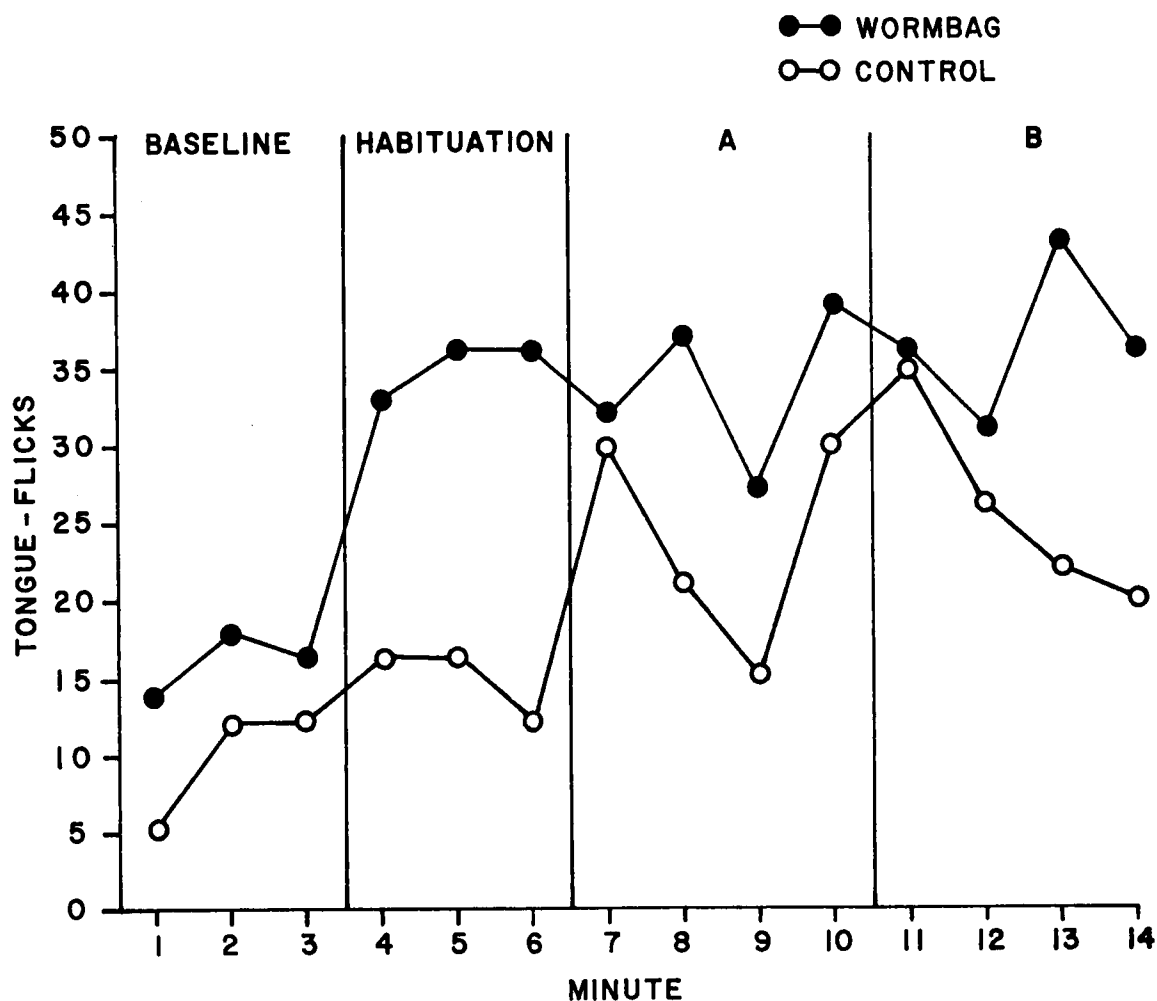


Figure 5. Tongue-flick rates for control bag and wormbag groups (plastic earthworm sections, Experiment 3).

in period B, both when control bag and wormbag conditions were in effect, open-mouthed attack occurred only twice in 128 minutes of exposure to plastic earthworm sections, and in both instances the sections were immediately released and not attacked again.

Conclusions

In garter snakes, open-mouthed attacks generally do not occur to moving prey in the absence of chemical cues, nor to diffuse chemical cues in the absence of contact with or visually-perceived movement of prey. When chemical cues are present attack infrequently occurs to moving objects free of prey odor. This suggests that a chemical cue on or very near the prey is involved in the actual elicitation of attack, but that with experience garter snakes will learn to attack moving objects on occasion, if volatile chemical cues are present. This is in agreement with findings by Sheffield, Law, and Burghardt (1968), who demonstrated that attack-eliciting components of water-based prey extracts are non-volatile.

Introduction of diffuse chemical cues from prey causes an increase in the rate of tongue-flicking; this illustrates the effectiveness of such cues in alerting the snake to the presence of prey and in initiating appetitive searching for food.² While opening a new

²Chiszar and his fellow researchers have demonstrated that for snakes placed in an unfamiliar (novel) environment,

section of the home cage to exploration did not cause a higher rate of tongue-flicking in the wormbag group than in the control bag group, the wormbag maintained this rate in the presence of movement while the tongue-flick of the control bag group began to decrease. This suggests that movement alone is not sufficient to maintain a high level of interest in foraging snakes.

rates of tongue-flicking are higher than for snakes which are returned to their home cages after handling (Chiszar and Carter, 1975; Chiszar, Carter, Knight, Simonsen, and Taylor, 1976; Chiszar, Scudder, and Knight, 1976; Chiszar and Simonsen, 1976; Chiszar, Radcliffe, and Scudder, in press). For garter snakes, the presence of food odors in the unfamiliar environment results in an even greater rate of tongue-flicking (Chiszar, Scudder, and Knight, 1976). For garter snakes rate of tongue-flicking is positively correlated with general activity (Kubie and Halpern, 1975).

CHAPTER V

DIFFERENTIAL PERFORMANCES OF A TONGUELESS

ADULT AND CONTROLS

A. Introduction

Snakes possess a vomeronasal or Jacobson's organ. This structure, which is present in other reptiles and in many mammals, is especially well-developed in snakes, and has become totally separated from the nasal cavity (Burghardt, 1970). Jacobson's organ lies below the nasal cavity, and opens into the anterior part of the palate by means of two lumina, or openings. The bifid tongue, which flicks in and out, seems to have an importance in chemoreception. It is not clear whether the tongue tips carry material directly into the lumina of the vomeronasal organ. Broman (1920), upon the basis of anatomical relationships, and Kahmann (1932), in tracing the course of carbon which had been placed on the tongue, concluded that the tongue tips were placed in the lumina. Wilde (1938), however, showed that garter snakes with severed olfactory nerves and excised tongues reacted to cotton swabs containing water-based surface extracts of prey, which were touched to the lips, with attack; control swabs containing water were not attacked. Wilde concluded that while the tongue

may aid in the transfer of material into the mouth, it need not carry the material to the vomeronasal organ. Kubie and Halpern (1977), established through use of radioactively marked earthworm extract that the tongue does transfer chemical stimuli to the lumina of Jacobson's organ.

A number of workers have attempted to assess the relative importance of olfaction and the vomeronasal sense by systematically eliminating use of the various senses. Kahmann (1932), Naulleau (1964, 1966), and Noble and Clausen (1936) found that trailing ability is abolished or impaired by blocking the nostrils. Cauterization of the vomeronasal organ or removal of the tongue also has this effect (Kahmann, 1932; Noble and Clausen, 1936). Wilde (1938) found that bilaterally severing the vomeronasal nerve tracts abolished the prey-attack response to chemical cues placed on the lips or tongue. Wilde's operated animals did not feed. This is in apparent contradiction to Noble and Clausen's (1936) findings that following cauterization of Jacobson's organ, snakes (genera Thamnophis and Storeria) did feed. Wilde, however, used dead (immobile) prey, while Noble and Clausen used living (moving) prey and apparently fed their snakes in groups. Burghardt (1970) has pointed out that factors such as social facilitation and conditioning, as well as cues such as movement of prey, may account for the differences found by these researchers. Burghardt's own research (Burghardt and Pruitt, 1975) indicates that

newborn garter snakes show almost total suppression of feeding following tongue removal, but that experienced snakes will resume feeding (Burghardt and Pruitt, 1975). An intact Jacobson's organ is also essential for courtship, feeding, and prey trailing in male garter snakes (Kubie and Halpern, 1977). This latter work definitively establishes through surgical manipulation the important role of the vomeronasal system.

B. Experiment 4

Given the importance of the tongue-Jacobson's organ system in the feeding of garter snakes, how would a snake with impaired functioning of this system respond to moving worm sections? The tongueless adult T. s. sirtalis used by Burghardt and Pruitt (1975) was still available for testing (it was being fed on a diet of earthworms). Its performance was compared to that of a normal snake.

Methods

Two snakes naive to the apparatus were tested; they were an adult female T. s. concinnus from northwestern Oregon and the adult female T. s. sirtalis used by Burghardt and Pruitt (1975). The tongue of this snake had been severed at a point 19 mm below the fork several years previously. Burghardt and Pruitt remarked that this snake became very aggressive after surgery; it remained so until its death several months after this series of experiments was completed.

This prey attack behavior of the sirtalis was unlike that of all other snakes tested. Rather than approaching its prey, pausing, and then lunging and seizing it, as normal snakes did, this snake opened its mouth and thrashed about until it encountered its prey.

Procedure. The snakes were presented with nonmoving paired with moving earthworm sections. Moving sections rotated at speeds 0.5, 4, 32, 256, and 2048 revs/minute. Sections were initially presented at 32 revs/minute. The order of speeds was then random, with the restriction that all speeds were presented before any speed was repeated. The snakes were run to a maximum of 20 trials daily, or until latencies for two consecutive trials exceeded 90 seconds. It was originally planned to run each snake for 50 trials, but because of the tongueless snake's bizarre feeding behavior I decided to test her for several additional days (a total of 75 trials).

Results and Discussion

At combined speeds the normal snake attacked the moving prey in preference to the nonmoving (39 attacks to moving, 20 to nonmoving, $p < 0.025$, binomial); the tongueless snake showed no preference for moving prey items (40 attacks to moving, 35 to nonmoving). However, both snakes chose prey moving at 32 revs/minute over nonmoving prey (12 and 11 to moving and 3 and 1 to nonmoving for the tongueless

and normal animals, respectively; $p < 0.025$, binomial, for each). Additionally, the control snake selected moving earthworm sections at 256 revs/minute and showed decreased latencies at 32 and 256 revs/minute (Figure 6). The tongueless snake showed no decreased mean latency at 32 revs/minute, the speed at which it preferred moving sections of worm. Latencies for the experimental snake were longer than latencies for the control ($p < 0.025$, t-test).

The differences in the performances of the two snakes seemed to be due to the peculiar feeding behavior of the tongueless T. s. sirtalis. Not only was the normal sequence of stalk and attack not evident in this snake, but the preference for moving earthworm sections was affected. However, it should be noted that the use of single subjects of two subspecies may have confounded these differences.

C. Experiment 5

The wormbag provided a strong competing source of the same odor as the earthworm sections (excluding differences caused by the scalding process). Would the tongueless snake respond differently to worm sections without the wormbag in place?

Methods

Subjects. The tongueless T. s. sirtalis and the T. s. concinnus which were used in Experiment 4 and two

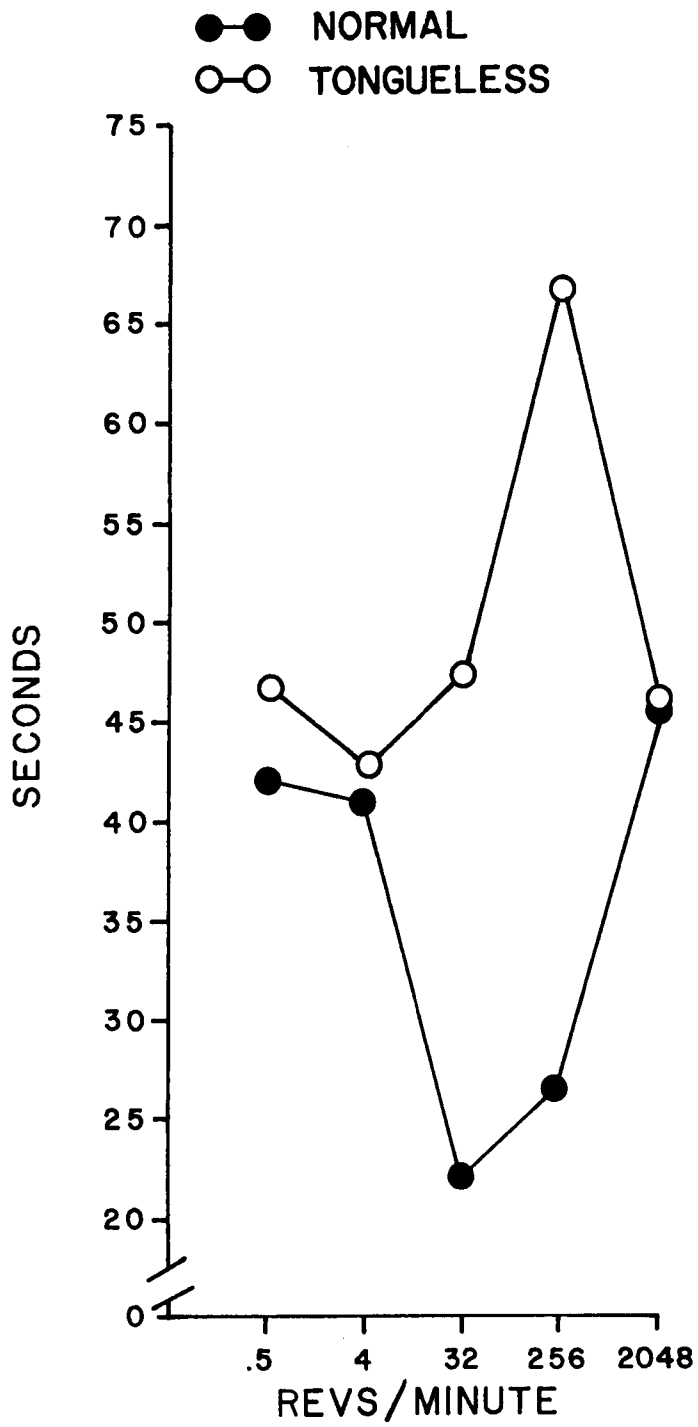


Figure 6. Mean latencies for individual snakes (Experiment 4).

other snakes which were familiar with our testing situation, a male and a female T. s. sirtalis collected in East Tennessee, with snout-vent lengths of 54 and 31 cm, respectively.

Procedure. The two normal T. s. sirtalis were tested with nonmoving prey items, first with a control bag in place (5 trials), and then with the wormbag present (5 trials). The remaining two snakes were presented with moving sections, first with the control bag present (5 trials), and then with the wormbag present (5 trials). Each snake received all 10 trials on the same day.

Results and Discussion

For all trials, the snakes that were presented with nonmoving worm sections attacked the section that was on the side of the test chamber on which they entered (16 attacks on the same side, 4 on opposite side, $p < 0.01$, binomial). This was not true for the snakes which were tested with moving worm sections (7 attacks on the same side, 13 on opposite side).

When the wormbag was in place, latencies were shorter for the normal snakes than when the control bag was in place (Table 5). Interestingly, however, the tongueless sirtalis had considerably longer latencies when the wormbag was in place ($p < 0.025$, Mann-Whitney U test). This further implicates this snake's tonguelessness as

TABLE 5
MEAN ATTACK LATENCIES (EXPERIMENT 5)**

Snake	Latency (secs.)		Worm Sections
	Wormbag	Control bag	
56 (tongueless)	66.0	38.9*	moving
33 (<u>T. s. con-</u> <u>cinnus</u>)	16.5*	28.8	moving
22	46.5	67.6	nonmoving
51b	38.8	84.4	nonmoving

* $p < 0.05$, Mann-Whitney U-test.

**based on 5 trials for each snake in each condition.

the major cause of the differences in the performances of the snakes in Experiment 4 (not forgetting the very small sample size).

Odor of prey seems to release appetitive behavior of searching (crawling around while flicking the tongue) in normal snakes. In the tongueless sirtalis odor of prey caused it to thrash about with open mouth. Once aroused, the normal snakes seemed to be able to follow a gradient of odor to their prey despite a strong competing source of the same odor. The tongueless snake seemed unable to do this. Instead, its feeding strategy seemed to be to cover the most possible territory with open mouth.

D. Conclusions

Olfaction seems to alert garter snakes to the presence of prey (Burghardt, 1969; Cowles and Phelan, 1958; Fox, 1952). This occurs without any active behavior on the part of the snake, during normal breathing. Once the snake is alerted, tongue protrusion brings the tongue-Jacobson's organ system into use; this system is important in following airborne and surface odors to their source (Baumann, 1927; Burghardt, 1969; Cowles and Phelan, 1958; Dullemeijer, 1961; Kahmann, 1932; Naulleau, 1964, 1966). Since normal transfer of particles to Jacobson's organ was disrupted in the tongueless snake, the abnormal feeding behavior may have been the best alternative method of

finding prey in the absence of the ability to trail prey by chemical means. The dependence of the garter snake upon chemical means of locating prey is evident in the tongueless snake by the disruption of its normal feeding pattern; it seemed less able than normal snakes to utilize visual cues in locating prey. In the normal snakes movement caused the snakes to approach, while the tongueless snake encountered the worm sections while thrashing about.

CHAPTER VI

DISCUSSION

Natricine snakes will often not attack moving prey without chemical cues being present, even after considerable feeding experience. There are exceptions to this, however (Drummond, in press). In the presence of prey odor, visual cues can direct garter snakes to the vicinity of moving objects, even when the odor comes from a different location in space. Attack does not occur to nonmoving objects if they are free of odor of prey and only rarely to odor-free objects which are moving. This suggests that a chemical cue closely associated with the prey, probably a non-volatile molecule, as determined by Sheffield, Law, and Burghardt (1968), is important in the actual elicitation of attack.

Different sensory modalities (visual and chemical) are important at different times during the feeding sequence of garter snakes. For example, chemical cues can alert the snake that appropriate prey is present (probably through olfaction) at considerable distances, when the prey may not be in sight, and may lower the threshold of responsivity to visual cues such as movement (Burghardt, 1969). The snake can then be directed to the immediate vicinity of the prey by chemical cues (probably through

the tongue-Jacobson's organ system), and visual cues, if available. Once the snake is close to its prey, visual cues such as movement direct its strike, allowing last-second compensations in direction and intensity. Chemical cues associated with the prey trigger the strike in slow-moving prey, but tongue contact or even close approach may be impossible for rapidly moving prey. In this case attacks without contact with non-volatile cues associated with the surface of the prey may be essential if the snake is not to miss a meal. If the strike is successful, chemical cues (probably through direct stimulation of the Jacobson's organ) by the prey and through gustation cause ingestion to occur; inappropriate objects are immediately released.

In the garter snakes I tested, rapidly moving but odor-free objects directed the snakes to their vicinity, even though chemical cues probably would have directed them elsewhere in the absence of movement. Thus, it seems that a "shift in reliance from one sensory modality to another" occurred; as in Herzog and Burghardt's racers, response to a visual cue led to a different response to chemical cues. Perhaps Curio's (1976) term "shift of attention" can be better described (or translated) in both cases, as well as in the cases of bolitoglossine salamanders (Roth, 1976) and rattlesnakes (Chiszar and Radcliffe, 1976; Chiszar, Scudder, and Knight, 1976; Chiszar, Radcliffe, and

Scudder, in press; Dullemeijer, 1961) as a "shift in reliance from one sensory modality to another."

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