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The Escape Behavior of the Cockroach *Periplaneta americana*

II. Detection of Natural Predators by Air Displacement

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Summary. 1. The escape response of the cockroach *Periplaneta americana* to the predatory strike of the toad *Bufo marinus* was studied by cinematography and stop-frame analysis. Various manipulations permitted us to appraise the role of the turning behavior mediated by the cercal wind receptors (Camhi and Tom, 1978) in the escape from toads.

2. Cockroaches with their cerci covered showed fewer successful escapes from toad strikes than did either normal cockroaches or those with their sternites covered as a control (Table 1).

3. The cockroach's escape behavior was similar to its behavioral response to wind puffs (Camhi and Tom, 1978). Similarities included an initial pivot away from the toad (Figs. 1 and 2) and similar initial movements of the metathoracic legs.

4. The displacement of air produced by a toad's strike was recordable at the position of the cockroach throughout essentially the entire strike. If wind were the only cue by which the cockroach responded to the toad, the cockroach must have received a suprathreshold wind stimulus at an average time of 75 ms before the toad's tongue appeared. This calculation is the sum of the average time during the strike when the cockroach began its escape movements (17 ms before the toad's tongue appeared [Fig. 4]), and the mean latency of the escape response to wind puffs (58 ms [Roeder, 1963; Camhi and Tom, 1978]). Therefore, the mean wind speed at 75 ms before the toad's tongue appeared should represent an adequate stimulus to evoke the escape behavior. The mean wind speed at this time was 22 mm/s.

5. Controlled wind puffs directed at the cerci of restrained cockroaches evoked escape movements of the legs. The mean value of the peak wind speed of a just supra-threshold puff was only 1–5 mm/s.

6. Visual, auditory, vibrational and olfactory cues from the toad, in the absence of wind, did not evoke escape behavior.

7. These results suggest that the extreme sensitivity of the cockroach's wind-detecting system permits the use of wind as a major channel of information for detecting predators under semi-natural conditions.

8. These findings are discussed with reference to (a) the problems this detection system might encounter in a natural environment (b) implications for the neural control of escape behavior in the cockroach, and (c) comparative aspects of escape behavior in different animals.

Introduction

The first paper in this series (Camhi and Tom, 1978) showed that the cockroach *Periplaneta americana* responds to a brief wind stimulus by pivoting its body away from the source of wind. This behavior is apparently mediated by wind-receptive filiform hairs located on the ventral surfaces of the cerci – two posterior abdominal appendages. The sensory neurons associated with these hairs excite 7 bilateral pairs of giant interneurons (Westin et al., 1977) which have been implicated in the control of the oriented evasive behavior (Ritzmann and Camhi, 1978; Camhi and Tom, 1978).

The present paper concerns the function which this turning response to wind might serve in the life of the cockroach. The turning response might be a way of escaping from approaching predators (Roeder, 1963). However, there is no evidence that the behavior can function in this manner. Indeed, we were uncer-

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tain whether the low wind speeds which we presume the cockroach would receive from an approaching predator would be adequate to evoke the turning behavior. Moreover, there is no a priori reason to believe that the pivot which the cockroach's body makes in response to a wind puff would be an effective dodge of a predator.

We report here an analysis of the behavioral interactions of *Periplaneta americana* with a natural predator, the toad *Bufo marinus*. Cockroaches often escaped successfully from these toads. Their escape behavior closely resembled their response to wind puffs (Camhi and Tom, 1978). We present evidence that wind produced by the movement of a toad during its predatory strike is the major cue which evokes the escape behavior. Moreover, analysis of the dynamics of the predator-prey interaction indicates that the cockroach's pivot is a behavior well adapted for escaping from the toad's strike.

Materials and Methods

We used adult male *Periplaneta americana* in all experiments. The rearing and care of the insects have been described (Camhi and Tom, 1978). As a predator on the cockroaches we used the toad *Bufo marinus*. Selection of this predator was based upon the following criteria: (1) this species of toad preys upon *Periplaneta* in nature (Roth and Willis, 1960). (2) Both predator and prey are tropical in origin, inhabiting the floor of the rain forest, and are nocturnal (Roth and Willis, 1960). (3) The toad's predatory strike is an unambiguous event, and therefore was easy for us to recognize. (4) The kinematics of the predatory strike of *Bufo marinus* have been studied in detail, providing valuable background information (Dean, 1977). The strike is highly stereotyped and therefore should generate fairly reproducible wind stimuli.

The toads were commercially supplied adult males and females weighing 250–385 g. They were kept at 25 °C, 50% relative humidity and on a 12:12 L:D photoperiod. They had constant access to water and were fed mealworms and crickets 1–3 times per week. Each toad was starved for 1–4 days prior to being used as a predator.

The interactions which we observed between toads and cockroaches took place in a circular chamber 1 m in diameter. This chamber, described in the previous paper (Camhi and Tom, 1978), was modified by extending the height of the walls to prevent the toads from jumping out. To begin a series of predator-prey interactions, a toad was placed in the chamber and the cockroach was kept in a separate container nearby, out of the toad's sight. Both animals were adapted to the lighting (see below) and other conditions of the experimental room for at least 30 min. Then the cockroach was gently introduced into the chamber on the side opposite the toad. The toad usually remained motionless while the cockroach explored the chamber. Only if the cockroach came within 10–15 cm did the toad strike. Occasionally, when a cockroach came within about 30 cm, the toad would walk slowly forward and then strike from a distance of 10–15 cm.

Some predator-prey interactions were carried out at 0.1–0.5 Lux (fluorescent illumination). This simulated the nearly fully moonlit conditions under which *Bufo marinus* often forages in nature (R. Jaeger, personal communication). These interactions were not filmed. Other interactions were filmed under either 500 Lux or 1500–3000 Lux illumination (tungsten bulb). The temperature at the floor of the chamber was 24–29 °C. We filmed at 64 frames/s using a Bolex H 16 reflex camera. The camera's view of the interaction, through a 45° mirror, was effectively from above (see Fig. 1 of Camhi and Tom, 1978).

To record the wind made by a toad during its predatory strike, we arranged for the toad to strike at a cockroach (anesthetized with CO_2) which was drawn across the chamber floor by means of a thread tied to its body. As a toad began to make orienting movements toward the cockroach, we brought the insect to rest at a position within 1 cm of the active element of a hot wire anemometer (Datametrix 800 VTP, Wilmington, Mass.). The cockroach did not move during the toad's strike. The wind speed, recorded by the anemometer, was displayed on a Tektronix 564 oscilloscope. The Bolex camera viewed the toad's strike and, through a mirror system, the oscilloscope. (The toad's view of the oscilloscope screen was blocked by a curtain.) Thus the ciné film record included both the instantaneous position of the toad with respect to the cockroach, and the instantaneous wind speed at the location of the cockroach. The wind recording was also stored on tape for subsequent analysis (Hewlett Packard 3960 Instrumentation tape recorder). The anemometer had a frequency response to air displacements of approximately 0–100 Hz, and the tape recorder had a frequency response of 0–2.5 kHz. Special problems encountered in recording very low wind speeds are described in the Appendix.

To determine the threshold wind speed for a behavioral response, controlled wind puffs of various velocities were directed at the cerci of restrained cockroaches. The wind stimulator used has been previously described (Westin et al., 1977). In about half of these experiments the insect was shielded from ambient air currents by surrounding it with a plexiglass cylinder, partially closed on top and bottom. For each of these experiments, a cockroach was fixed in place on the surface of a plastic petri dish. We made a small hole in the lid of the dish and filled the volume of the dish with Sylgard resin. After clipping the wings to about half their length, we secured the insect to the lid of the petri dish by placing four pins vertically through the left and right tergal margins of two abdominal segments. and then into the Sylgard. The upper surface of the dish was lightly lubricated with oil, permitting the cockroach to make essentially normal walking movements while fixed in place. Any insect which groomed its cerci with its legs was not used, as this raised the possibility that oil would be applied to the cercal hairs. Wind velocities were determined before and after each experiment by recording with the hot-wire anemometer, whose probe was placed at the location of the cerci.

Results

We carried out the following experiment in order to determine whether cercal receptors provide the cockroach with information useful in escaping from toads. A single toad was introduced into the observation chamber which was illuminated with an intensity of 0.1–0.5 Lux. After approximately one-half hour, we gently introduced a dark-adapted cockroach into the opposite end of the chamber. We counted the number of strikes made by the toad and the number of successful escapes by the cockroach. In all, we used 5 toads and 66 cockroaches. Each cockroach tested belonged to one of three categories: (1) normal

Table 1. Success of three categories of cockroach in escaping from predatory strikes of the toad *Bufo marinus*. Cockroaches with cerci covered escaped significantly less frequently than normal or control cockroaches (see text for details). As is shown, this result was obtained by analyzing either the number of strikes from which there was an escape by cockroaches of each category, or the number of cockroaches of each category which escaped at least once. Statistics: Mann Whitney test

Success of cockroaches in escaping from toads				
Category of cockroach	No. of escapes / No. of strikes	(%)	No. of cockroaches which escaped at least once / No. of cockroaches tested	(%)
(1) Normal	24/44	55	10/21	48
(2) Cerci covered	2/24	8	1/22	5
(3) Control	17/36	47	8/23	35
	1 vs. 2 $p<0.01$ 2 vs. 3 $p<0.01$ 1 vs. 3 $p>0.05$		1 vs. 2 $p<0.01$ 2 vs. 3 $p<0.05$ 1 vs. 3 $p>0.05$	

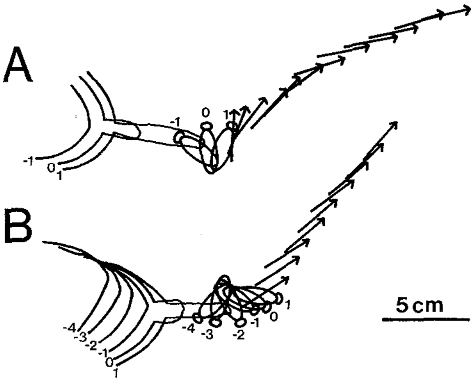

Fig. 1A and B. Ciné sequences of 2 toad-cockroach interactions. For each interaction, front of toad's head and tongue are traced from a series of ciné frames. Tracings are numbered with reference to the frame on which toad's tongue first appeared (frame 0). The earliest frame shown in **A** and **B** is that just before the cockroach began to move (thus the initial part of the toad's tongue is not shown). On the first several frames, until the tongue reaches its most extended position, the cockroach's outline is drawn; subsequently the positions of the cockroach's body are indicated by arrows. Numbers beside the outline of each cockroach indicate ciné frames, corresponding to the numbers on the tracings of the toad

cockroaches; (2) those which had both their cerci covered with wax; (3) those which had an equivalent or greater amount of wax placed on their abdominal sternites but not on their cerci (control animals). The wax was applied without any anesthesia on the day prior to testing. On a given day, each toad was presented one of each type of cockroach in a quasi-random sequence[1]. After a cockroach was captured by a toad, we waited approximately 2 min before introducing the next insect. Cockroaches which made 5 successful escapes were removed and not used again.

Normal and control insects escaped significantly more often than those with their cerci covered (Table 1). Among the cockroaches with their cerci covered, there were only two escapes (out of 24 strikes), both by the same insect. (It is possible that this individual's cerci had become partially uncovered. However, we could not check this, as the insect was captured and eaten on the third strike.) The results of this experiment suggest that receptors on the cerci, presumably those of wind-receptive filiform hairs, are useful in detecting the approach of the toad and initiating escape.

Next we filmed, under 500 Lux illumination, a set of predator-prey interactions to see whether the cockroach's response resembled its response to wind puffs. It is known that in response to a wind puff, the cockroach makes an initial pivot away from the wind stimulator. The fixed point about which the body pivots is located somewhere in the posterior region of the body (see Fig. 3 of Camhi and Tom, 1978).

Figure 1 shows two examples of successful escape responses to toad strikes. In each case, the cockroach's initial movement is a pivot away from the toad, with the pivot point located in the posterior region of the body. In fact, out of 19 successful escapes, 18 showed initial turns away from the toad (Fig. 2)[2]. All the encounters in Fig. 2 occurred with the cockroach almost facing the toad (angle of toad to cockroach was between 90° and 180°; where by convention, 180° is directly in front of the animal.) This reflects the fact that the toad usually remained stationary, so that encounters occurred only when a cockroach approached a toad.

Not only did the cockroaches turn away from both the wind stimulator and the toads, but they used similar leg movements to execute both turns. Cockroaches characteristically respond to wind puffs from the angles 90° left to 180° with an initial protraction of the left metathoracic leg and a fixing of the right metathoracic leg firmly against the ground. (The tarsus of the right leg, which is located near the poste-

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[1] The sequence was determined by a table of random numbers. However, a given toad on a given day was presented with only one of each category of cockroach. For instance, the random number sequence 2-1-2-2-1-3 resulted in the presentation sequence 2-1-3

[2] In this series of encounters 16 captures of cockroaches by toads were filmed. In 11 of these, the cockroach made no movement prior to its capture, and in 3 of the remaining 5, the cockroach turned *toward* the toad

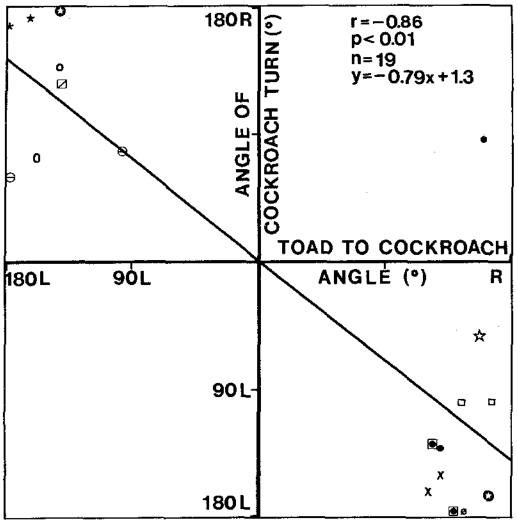

Fig. 2. Angle of turning response of free-ranging cockroaches to predatory strikes of toads. Definitions: angle of toad to cockroach (abscissa), 0° = toad's strike from behind cockroach; 180° = head-on encounters. Angle of cockroach's turn (ordinate), 0° turn = forward locomotion; 180°R = about face to right; 180° L = about face to left. (See also Fig. 4 of Camhi and Tom, 1978.) Each type of symbol represents the response of a different animal. All the data points are for relatively large angles of strike because most of the encounters occurred when an insect walked toward a toad. Slope of regression line is larger than for responses to wind puffs (Camhi and Tom, 1978). This may be because only turns of cockroaches which successfully escaped from the toads are plotted here; the captured cockroaches might have been those making smaller turns

rior end of the abdomen in the normal standing posture, serves as the pivot point for the behavior.) Wind from 90° right to 180° gives the opposite response (Camhi and Tom, 1978). Of the 7 successful escapes on which the legs were clearly visible, all of which were within this range of stimulus angles, all 7 involved this pattern of initial movements by the metathoracic legs.

The similarity of the cockroach's turning and leg movements during responses to both wind puffs and toad strikes lends support to the idea that wind made by the toad's movement may serve as a cue for the escape behavior. However, it was necessary to verify that a cockroach could detect a wind of this sort. Therefore, we analyzed the wind made by the toad's movement during a strike, synthesized the initial part of this signal with a wind stimulator, and delivered it to the cerci of restrained cockroaches to see whether they responded behaviorally.

To measure the wind from a toad's strike, a cockroach immobilized with CO_2 was drawn along the chamber floor by a thread, to a region within 1 cm of the anemometer's active wire. The wire was at the same height above the substrate as are the cerci in a standing cockroach. The toad's strike, as well as the oscilloscope's record of instantaneous wind speed at the cockroach, were recorded on ciné film as described in the methods section. Figure 3A shows, for a single representative strike, simultaneous plots of the position of the front of the toad's body, and the wind recorded at the cockroach. The strike lasted approximately 250 ms (16 ciné frames) although the toad's tongue ("T" in Fig. 3A) contacted the cockroach after only about 200 ms. These durations are comparable to those reported previously, where the mean time from the start of the toad's movement until the tongue contacted its prey was 180 ms (Dean, 1977). The toad's movement covered a total of about 14 cm. Throughout almost all of the strike, a measurable wind signal occurred at the cockroach (Fig. 3A).

It was then necessary to determine whether the wind speed at the cockroach was adequate to evoke an escape response. However, the wind speed changed throughout the strike. Therefore, it was essential to determine by what moment a cockroach, which escaped successfully, had received an adequate wind stimulus to do so. In the successful escapes which we had filmed, cockroaches began to turn away from the toads at a mean time of 17 ms (1.1 ciné frames) before the toad's tongue emerged from its mouth (Fig. 4). (This moment is indicated by arrow "d" at the bottom of Fig. 3A.) The mean latency of the escape response has been measured as 54 ms (Roeder, 1963) and 58 ms (Camhi and Tom, 1978). Thus if the toad's wind were the *only* cue used by the cockroach, supra-threshold wind speed should have occurred by roughly 3.5 ciné frames (= 55 ms) before the cockroach's first movement; that is, roughly 4.5 frames before the toad's tongue emerged (arrow "c" of Fig. 3A). The wind measured at the cockroach at this moment during 19 strikes had a mean speed of 0.02 m/s (s = 0.01).

To determine whether a cockroach would respond behaviorally to a wind puff with a peak speed of 0.02 m/s we restrained the insect on a lubricated petri dish as described in the methods section. The position and height of the cerci were normal. The dish was positioned with the cerci 2 cm in front of the tube of the controlled wind stimulator (described in Westin et al., 1977). About one-half of the insects so treated appeared essentially normal, making walking movements which were well coordinated in the typical tripod pattern. Animals which did not walk normally were not used. The most common stepping frequency was approximately 3/s. Prolonged periods of walking usually continued for more than 4 h, with short (1–10 min) bouts of walking separated by pauses of a few seconds to less than a minute. Wind puffs of

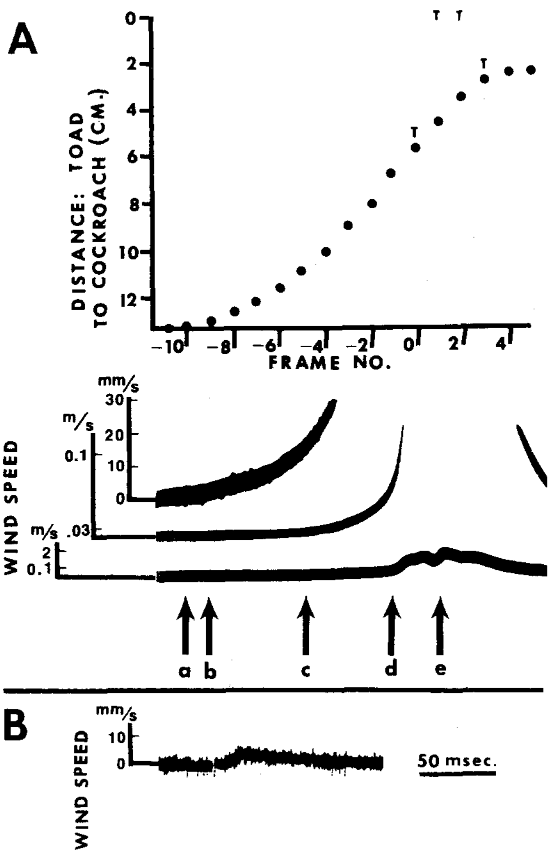

Fig. 3. **A** The strike of a toad; simultaneous records of position of toad and wind recorded at the location of the cockroach. *Top graph:* distance from front-most part of toad's body to the cockroach on successive frames. *T*, position of tip of protruded tongue. Frames are numbered with reference to that frame on which toad's tongue first appeared (frame 0). *Bottom 3 traces:* wind recorded at cockroach at low (bottom), medium (middle) and high (top) sensitivities. Time scale same as for top graph. Wind produced by the toad was recorded throughout essentially the entire strike. Arrows below wind traces indicate the following moments during the strike: *e*, moment tongue hit cockroach; *d*, mean time (relative to frame 0) that successfully escaping cockroaches began to move in response to strike; *c*, 58 ms before *d*. (58 ms is the latency from our previous measurements [Camhi and Tom, 1978]); *b*, moment when threshold wind speed arrived at cockroach (see below); *a*, moment when toad's movement was first detectable. **B** A just supra-threshold wind puff, produced by wind stimulator. Recorded at same sensitivity as the uppermost of the 3 wind traces in part **A**. The puff is preceded by a very brief electrical artifact. Time scale same for parts **A** and **B**

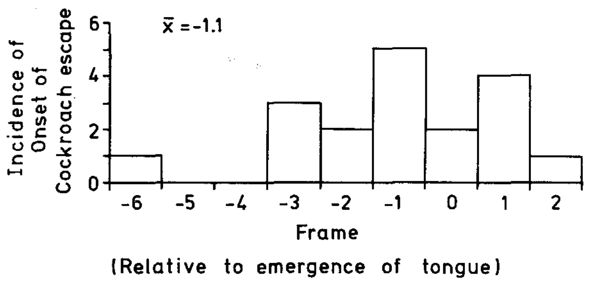

Fig. 4. Times of onset of cockroach evasive behavior during toad strikes. Time is indicated in ciné frames (each 15.6 ms) relative to the first frame on which toad's tongue appeared (frame 0). Mean time of onset was 1.1 frames (17 ms) before tongue appeared

various peak speeds were delivered to each of 11 cockroaches during, and just following, bouts of walking. All inter-stimulus intervals were at least 2 min.

For each of the 11 animals we determined the threshold stimulus, operationally defined as the smallest puff which evoked any detectable running or startle movements of the legs on at least 50% of the trials. Although we have not characterized these leg movements in detail, they were easy to recognize because of their abrupt nature. Only occasionally was it difficult to distinguish between ongoing walking movements and a response to the stimulus. Such questionable data were not included in our analysis. (Qualification of our definition of threshold is presented in the Discussion).

The peak wind speed of a just supra-threshold puff had a mean value of 0.003 m/s (Fig. 3B)[3]. There was no systematic difference between the threshold determined during walking and that during the first half second of a pause. This threshold wind speed was less than the wind speed produced by the toad's strike at 4.5 frames prior to the emergence of its tongue (arrow "c" of Fig. 3A; mean = 0.02 m/s). The moment that the speed of the toad's wind reached this threshold wind speed is indicated by arrow "b" in Figure 3A. This occurred when the front of the toad's body was still 13 cm from the cockroach ($\bar{x}$ = 9.8 cm; s = 2.5 cm).

Measurement of wind speeds in this low range could incur errors as great as 20–40% (see Appendix). Therefore, the cockroach's threshold was somewhere between 0.001–0.005 m/s. These tests were made with puffs delivered from 0° (directly behind the cockroach). However, we confirmed that puffs from 135° left or right gave essentially the same value of threshold. All responses to wind by these restrained cockroaches were obliterated when we covered the cerci with petroleum jelly.

Thus cockroaches responded to wind stimuli whose peak speed was lower than that which they received from the toad at the time by which they were calculated to have first detected the toad's wind. This suggests that wind is a sufficient stimulus for the cockroach to respond to the onset of a toad's predatory strike. In fact, we often saw cockroaches

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[3] Peak wind speeds two to four times higher were necessary to evoke consistently strong running responses

turn and run away when a nearby toad made a brief orienting movement of its head or body. Though we did not record the wind speeds produced by these smaller movements of the toad, it is possible that they too were within the range of the cockroach's sensitivity.

Additional observations suggest that numerous other potential cues in fact played little or no role in evoking the escape behavior. In most strikes, the toad was beyond the tips of the cockroach's antennae at the moment when the evasive behavior began. Thus direct tactile stimulation was not involved. Cockroaches often walked on top of, and rested upon, toads which did not strike, suggesting that olfactory cues or the sight of a stationary toad did not repel the insects. Sharp taps to the under-surface or side of the chamber, which resulted in much more audible sounds and apparently much greater substrate vibrations than occurred during the toad's strike, evoked no evasive or other obvious behavior. In addition, cockroaches showed little or no response to toads striking from behind a transparent barrier, indicating that visual cues were not of major importance in the escape behavior. The barrier consisted of a shock-mounted plexiglass plate, separated by about 1 cm from a glass plate which was sealed tightly with lubricant to the floor and walls of the chamber. Toads made strikes which were of normal appearance at cockroaches on the opposite side of the barrier. In doing so, a toad collided with the plexiglass plate usually at a location less than 3 cm away from the cockroach. Based upon data like those of Figure 1, we estimated that, had the barrier not been present, over 50% of the cokroaches would have responded by the time the toad had approached within these 3 cm. 52 strikes from behind the barrier at 4 cockroaches tested individually under 0.1–0.5 Lux illumination evoked no detectable behavioral responses. At 500 Lux, out of 33 strikes made at 7 cockroaches, 3 strikes were followed by running movements which could not be ruled out as visually evoked responses to the toad. Cockroaches never responded, at 0.1, 500 or 3,000 Lux, to hand-held objects of various sizes, shapes and colors which were made to approach rapidly and collide with the plexiglass barrier.

Additional analysis of records like those of Fig. 3A indicated that there was only a short interval from the start of the cockroach's movement till the moment that the toad's tongue arrived at the cockroach's initial position (arrows d to e, Fig. 3A). The mean time for 18 encounters was 33 ms (2.1 frames). During the first 2.1 frames of a cockroach's response, its body movement consisted almost exclusively of rotational, and not translational, motion (Fig. 1). Thus it was this initial pivot, and not the subsequent running movements, which were responsible for the successful escapes. The toad almost always directed its tongue at the position of the head of the cockroach. The tongue usually overshot the initial position of the cockroach's head. From movement records like those of Figure 1, it is possible to calculate for a given toad-cockroach interaction the "safety margin" of the cockroach's response. For instance, in Fig. 1A, if the cockroach had delayed its response by the duration of 1 ciné frame (16 ms), the cockroach would have been struck by the tongue; this is a safety margin of 0 frames. In Fig. 1B, a delay of 1, but not of 2 frames, would still have permitted escape; this is a safety margin of 1 frame. The safety margins for most of the successful escapes which were clear enough to analyze were 0 or 1 frame (Fig. 5). Thus most of the successful escapes were "close calls". This underscores the importance for the cockroach, on approaching a predator, of making initial turns which have a short latency, large angular velocity and large total angle.

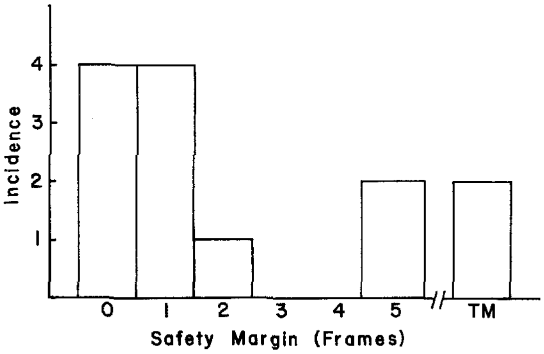

Fig. 5. Safety margins of cockroaches which escaped from toads. Safety margin (defined in text) is measured in frames, each 15.6 ms in duration. TM = total misses (i.e. the toad's strike was so inaccurate that it would have missed even if the cockroach hadn't moved.) The following uncertainties apply to the definition of safety margin: (1) the tip of the toad's tongue may have progressed somewhat farther during the camera's inter-frame period than shows on the film; (2) the toad's tongue could have contacted the cockroach's legs even though it didn't reach the body. The images of the legs on the film were usually blurred after the movement had started, so their positions could not be accurately determined. Both of these factors would lead to a lower safety margin than was measured. (3) It is unknown whether cockroaches which are contacted by the tongue are always eaten. Safety margin was determined solely on the basis of whether contact would have been made by the tongue

Discussion

The major conclusion of this paper is that the wind produced by the strike of a toad is adequate to evoke escape behavior in the cockroach. This conclusion is based upon the following four findings: (1) covering the cerci, which contain the wind-receptive hairs, decreased the cockroach's success at escaping from toads. (2) The cockroach's turning response to toads closely resembled its response to controlled wind puffs (Camhi and Tom, 1978). (3) Tactile, visual, olfactory, auditory and vibrational cues from the toad appeared to be unable, in the absence of wind, to evoke escape behavior. (4) The threshold wind speed for evoking the escape behavior was lower than the wind speed which the toad generated (Fig. 3).

The Low Threshold for Wind

The very low value of threshold wind speed which we measured raises a number of important issues. First, since the threshold measurements were made on cockroaches which were pinned in place and whose wings had been clipped, it is unclear how the values obtained relate to the threshold of free-ranging cockroaches. However, it is unlikely that pinning and removing the wings made the insects *more* sensitive to wind, since additional dissection of pinned animals makes them *less* sensitive to wind. Specifically, during experiments in which we recorded from the nerve cord, making an incision in the abdominal tergites, removing the gut, and cutting tracheoles and peripheral nerves in the mid-abdomen each led to a step-wise increase in the threshold wind speed (Camhi, unpublished observations). Therefore, the threshold of free-ranging cockroaches may actually be lower than the values obtained on pinned animals.

The low value of threshold also implies a need to re-evaluate the latency of the escape behavior. Our earlier latency measurements were made with puffs whose wind speed increased from 0 to 2 m/s in about 40 ms. The mean latency was 58 ms (Camhi and Tom, 1978). Roeder (1963) obtained a mean latency of 54 ms, using tethered cockroaches and unknown (but probably high) wind speeds. However, in the present experiments, the mean interval from the arrival of "threshold" wind at the cockroach to the onset of the escape behavior (e.g. arrows b to d of Fig. 3A) was 120 ms. This long latency could result from the low initial wind speed produced by the toad, though we have no direct evidence that wind speed effects latency. The discrepancy in the latency value points to the need to make such measurements using stimuli which the animal would experience in nature.

A third implication of the low threshold value concerns the possible role of the giant interneurons (GI's) in mediating the escape behavior. It is known that electrical stimulation of individual GI's evokes action potentials in leg motor neurons (Ritzmann and Camhi, 1978). However, in order to obtain a response from leg motor neurons, it was necessary to excite in a GI high frequency trains of action potentials. Trains of 4–32 action potentials at frequencies of 230–400 s^{-1} were used. Such high frequency stimuli mimicked the responses of the GI's to the wind stimuli which were used in most earlier experiments in this laboratory – puffs with peak wind speeds of 2.6 m/s (Westin et al., 1977).

The present paper shows, however, that evasive behavior is evoked by wind speeds three orders of magnitude lower than this. At these low speeds, fewer GI action potentials would be elicited. At the lowest speed which was formerly tested, 0.01 m/s[4], most or all of the GI's were still excited and retained their directional characteristics (Fig. 8 of Westin et al., 1977). Puffs with peak wind speeds less than 0.003 m/s evoke a brisk train of action potentials in recordings from the whole nerve cord with hook electrodes. Many of these action potentials are of the same amplitudes as the largest spikes evoked by stronger puffs (Camhi, unpublished). Therefore at least some GI's appear to be activated at wind speeds even below the behavioral threshold. Nevertheless, in the only experiments which provide evidence that the GI's drive the leg movements of the escape response, individual GI's had to be stimulated with many more action potentials than they would give in response to a just supra-threshold wind stimulus. It is known, however, that a wind puff from any direction would activate approximately 8 GI's (Westin et al., 1977). The outputs of some of the GI's may sum together at the motor or at a pre-motor level. Also, the minimal disturbance required to test the insect's behavioral threshold (4 pins in the abdomen and clipping the wings) has a much less depressive effect on the threshold than do the radical dissection and pinning of the legs which are required for intracellular experiments (Camhi, unpublished observations). Therefore, presumably fewer action potentials in a given GI would be required to evoke action potentials in leg motor neurons in the intact insect than in a radically dissected insect. In sum, the low behavioral threshold does not preclude a role for the GI's in mediating just supra-threshold escape responses. In fact, it suggests that the cockroach can determine the direction of a wind source from stimuli which excite at most a few action potentials in any one GI (Westin et al., 1977).

A fourth implication of the low wind speed to which the cockroach responds is that in nature it

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[4] The lowest wind speeds reported in the earlier studies in the laboratory were subject to considerable inaccuracies. This is because special problems associated with recording in this low range were not appreciated at that time (see Appendix)

might be difficult for the insect to discriminate between a wind current generated by an approaching object (i.e. a "signal") and ambient wind (i.e. "noise"). In the cockroach's original natural habitat, the tropical rain forest (Roth and Willis, 1960), environmental winds are effectively shielded by the forest canopy. For instance, in daylight when the mean wind speed at the level of the tree-tops is 1 m/s, mean wind speed at 2 m above ground level is approximately 10 cm/s. At ground level, where cockroaches would encounter toads, wind speed should be considerably lower, owing to the boundary effect of the ground. At night, when the cockroach is active, wind speeds are usually lower than during the day, and include less convective turbulence (Allen et al., 1972).

Nevertheless, wind speeds in excess of the cockroach's behavioral threshold (1–5 mm/s) probably do occur at ground level at night. Therefore, it would be important for the insect to be able to discriminate signal from noise. In fact, it appeared that the cockroach could make such discriminations in the laboratory. In about half of the experiments which we performed to measure the cockroach's threshold, we made no attempts to shield the insects from ambient wind currents in the room. The anemometer indicated that ambient wind speed was often several times greater than the threshold speed of our controlled wind puff. Yet the cockroach did not respond to these room currents. A notable feature of these currents was that their maximal acceleration was roughly 1/10 that of the puff stimulus. This raises the possibility that the cockroach's discrimination may consist in part of detecting differences in the acceleration of signal and noise. Such differences can be expected to be found in the natural habitat.

On theoretical grounds, ambient winds recorded a few millimeters above a surface should contain only frequency components below some upper frequency limit. Given the low wind speed (Allen et al., 1972) and the rough terrain, the upper frequency limit has been calculated as approximately 1 Hz[5]. The entire range of frequencies from 0–1 Hz has not been recorded. However, a power spectrum covering the range 0.001–0.1 Hz measured at 2 m above the ground in a tropical rain forest shows a peak at 0.01 Hz and a decline above this frequency. The peak amplitude was 10 cm/s (Allen et al., 1972). Therefore, the major component of wind acceleration was no greater than 2 mm/s^2. By contrast, the acceleration of the toad's wind at the moment when threshold wind speed was achieved was approximately 100 mm/s^2 (Fig. 3A). Therefore, some part of the neuronal network mediating the escape behavior may be selectively responsive to these higher accelerations.

A similar instance of discriminating sensory signals from background noise by the rate of increase of the signal has been reported in the crayfish escape system. The crayfish giant interneurons, which evoke escape behavior, are selectively responsive to tactile stimuli of rapidly increasing intensity (Wine and Krasne, 1972). In a related example, the caterpillar *Barathra brassicae* uses filiform hairs very much like those of the cockroach to detect the air displacements created by the wing beat of a predatory wasp. *Barathra* is selectively responsive to periodic displacements in the frequency range of the wasp's wing beat (Markl and Tautz, 1975; Tautz, 1977).

Dynamics of the Escape Movements

The cockroach's escape behavior began consistently with a pivot away from the toad (Figs. 1 and 6A). Translational movements did not begin until 50–75 ms after the onset of the pivot. One might have expected that the animal's initial response would be to run straight ahead, since this would eliminate the time-consuming pivot, and perhaps be the quickest way to avoid the toad's strike. However, as can be seen from Figure 6B, purely translational forward movements would probably be an ineffective strategy, since the entire length of the body would have to pass through a danger zone before the insect would be safe. This danger zone is defined by the outline of the toad's tongue at its most extended position (Fig. 6B). This argument applies most clearly for encounters where the toad struck at the cockroach's head and the angle of approach was nearly head-on. Both these conditions were met for most of the interactions studied (Figs. 1 and 2).

Another possible strategy is that diagrammed in Figure 6C. Here, by turning initially toward the toad, the cockroach would bring its entire body out of the direct line of the tongue's movement. The extent of the initial movement in the direction toward the toad would be small for large initial angles between cockroach and toad (that is, nearly head-on encounters). Therefore, this strategy would seem to be a good one for the largest angles, but for smaller angles (say, 135° or less) the movements of Figure 6A would be better.

In fact, the strategy of Fig. 6C is probably not a very good one. This is suggested in part by the fact that 3 out of 4 filmed encounters in which cockroaches made such turns resulted in captures by the toad[2]. The initial toad-to-cockroach angles for these 3 encounters were 144°, 167° and 177°. Moreover,

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[5] We are indepted to Dr. Z. Warhaft of the Department of Mechanical and Aerospace Engineering, Cornell University, for these calculations

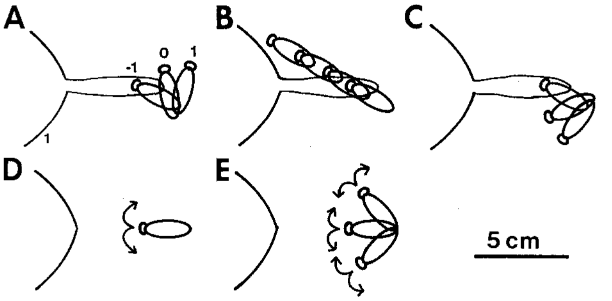

Fig. 6A–E. Alternative strategies of escape. **A–C** Three different possible escape strategies. In each case, a single outline of the toad and its extended tongue is shown. **A** A retracing of toad position 1 and cockroach positions −1 through 1 from Fig. 1A. **B** An alternative hypothetical strategy involving only forward translational motion by the cockroach. **C** An alternative hypothetical strategy involving a turn in the direction opposite to that of part **A** above. The sequence shown is the mirror image of that in part **A**. **D–E** Those angles of cockroach to toad at which the cockroach must decide between a large turn to the left and a large turn to the right (arrows). **D** For strategy **A** above, there is only one such angle. **E** For strategy **C** above there are 3 such angles. (See text for fuller explanation.)

this strategy would greatly complicate the cockroach's decision as to which direction to turn for a given stimulus. This is because there would be three different angles (Fig. 6E) rather than only one (Fig. 6D) at which the cockroach would face a decision whether to make a large turn to the left or a large turn to the right.

These factors indicate that the initial pivot which the cockroach makes in response to the toad is a highly adaptive movement. We have no information as to how the cockroach moves in response to other potential predators. Nevertheless, since the cockroach encounters toads in nature (Roth and Willis, 1960), and since we have seen this behavior actually save the insect's life, we surmise that there may have been considerable selective pressure on the cockroach to evolve specialized sensory, central and motor mechanisms to produce the turning response described here and in the preceding paper (Camhi and Tom, 1978). Since the wind receptor cells of the cerci, and at least some of the giant interneurons, have been implicated as mediating this response (Camhi and Tom, 1978; Ritzmann and Camhi, 1978), future physiological experiments on these neurons should take account of the particular specializations of this system. These specializations would include the very low threshold wind speeds, turns of different directions (and therefore different motor outputs) in response to different directions of wind, and discrimination between wind "signal" and "noise" possibly on the basis of wind acceleration.

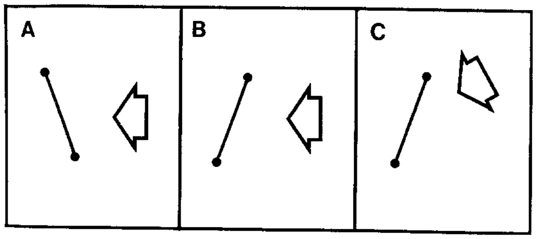

Fig. 7A–C. Calibration of anemometer at low wind speeds. 3 different orientations of anemometer's active wire and direction of flow are shown. In all 3 cases, both wire and direction of flow are pictured as though within the plane of the page. Orientation shown in **B** was used in these studies. See text for details

Appendix

Special problems are encountered in measuring wind speeds lower than about 1 cm/s. In this range, the output voltage of the hot-wire anemometer varied with the angle of the hot wire with respect to the vertical axis. If the upper part of the wire tilted away from the source of wind (Fig. 7A) the wind produced a negative output voltage from the anemometer, rather than the expected positive voltage. This may be because convectively heated air above the wire was blown back over the wire, heating it instead of cooling it. When the upper part of the wire was tilted into the wind (Fig. 7B), the convectively heated air above the wire should be blown away, and air of room temperature should be blown over the wire, thus cooling it. In this configuration only positive output voltages were recorded. This effect of angle was not encountered at higher wind speeds which would rapidly remove heated air from the region of the wire.

The anemometer was calibrated in the range 0–30 mm/s by moving the probe at measured speeds through still air in a closed plexiglass box. The movement was produced by an electric kymograph (Harvard Apparatus Co.) whose shaft passed through holes in the top and bottom of the box. Within the range of wind speeds tested, the output voltage varied by approximately 30% per 10° change of tilt away from a tilt of 20° with respect to the vertical axis (orientation of Fig. 7B). We used a 20° tilt in all measurements of low wind speeds. Measurement error was approximately ±20% for this angle. For a given angle of tilt of the wire with respect to the vertical axis there was less than ±20% variation in output voltage as the angle of the wind delivery tube was varied vertically by up to 30° (Fig. 7C) *and* horizontally by ±30°. Variations in the angle by which the toad approached the probe were less than 30° in each axis.

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