

Path integration in cockroach larvae, *Blattella germanica* (L.) (insect: Dictyoptera): Direction and distance estimation

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The question of how an insect finds its way between foraging areas and its shelter has been investigated in cockroaches, *Blattella germanica*. Our aim was to demonstrate that they integrate the characteristics of their outward trip to estimate direction and distance, which enable them to return to their shelter, relying on path integration mechanisms using kinesthetic cues. The return path pattern was characterized by a nearly linear oriented-to-the-goal trajectory, an arrest, and a systematic search at a much slower speed. The arrest position indicated that the insect's home vector was back to zero and that it was the estimated shelter position. If the shelter failed to be at the arrest position, cockroaches started a nonrandom systematic search directed mainly around the arrest. They looped back and forth around the arrest position and increased the size of their loops with time. The pattern of this search seems to be an ubiquitous trait in insects.

Navigation is the process of determining and maintaining a trajectory from one place to another. It includes choice of direction toward the goal and estimation of the distance to travel to reach it (Gallistel, 1990). The question of how an insect finds its way between a resting place and foraging areas has been investigated mainly with social hymenopterans, honeybees, and desert ants. Invertebrates have been shown to use two main navigation processes: path integration relying on short-term memory and learning of salient environmental visual cues, which involves long-term memory (Beugnon, 1986).

Path integration (also called dead reckoning) is considered by Wehner, Michel, and Antonsen (1996) to be the insect's fundamental system of navigation. It provides an individual, at any moment, with a continuous egocentric representation of its position in relation to its starting point (Mittelstaedt & Mittelstaedt, 1982; Wehner & Wehner, 1986). By measuring and integrating angular changes in direction and distances traveled between each change of direction, an animal can return to its shelter in a direct line rather than follow its tortuous outbound path in reverse. Analysis of this process has given rise to models formulated in terms of vector operations (Müller & Wehner, 1988). Direction and distance to the shelter are given by a single vector with egocentric coordinates; its orientation indicates direction, and its length indicates distance. As an animal nears its shelter, the vector decreases and, finally, is reset at zero when the animal is back in its shelter. Therefore, the vector is forgotten

every time the animal returns home (Wehner & Srinivasan, 1981).

With path integration mechanisms, position is calculated with the help of external references or allothetic information in bees (Dyer & Dickinson, 1994; von Frisch, 1967), ants (Duelli & Wehner, 1973; Santschi, 1911; Wehner & Müller, 1993), desert isopods (Hoffmann, 1984), and crickets (Beugnon & Campan, 1989). These species use celestial cues to estimate their position, using an innate knowledge of the ephemeris function (pattern of daily and seasonal change of the sun's azimuth) or of the electric vector (E-vector) pattern of polarized light in the sky (Wehner, 1983). Other species use internal references, such as kinesthetic, vestibular, and visual flow information (Mittelstaedt & Mittelstaedt, 1982), which are called idiothetic cues. Spiders estimate their position, relative to their shelter, using kinesthetic information gathered while moving and transmitted via exoskeleton proprioceptors located in their legs (Görner & Claas, 1985; Seyfarth & Barth, 1972; Seyfarth, Hargenvioder, Ebbes, & Barth, 1982). Idiothetic cues are also used by night-active rodents, which integrate internal vestibular changes to compute their position modifications (Séguinot, Maurer, & Etienne, 1993).

Cockroaches are an interesting species with which to investigate navigation mechanisms, for several reasons. German cockroaches, *Blattella germanica* (L.) (Dictyoptera: Blattellidae), behave like central place foragers, returning to their shelter after each foraging trip (Rivault, 1989). They live in social congregations and display a variety of interindividual behaviors necessitating active information transfer (Parrish, Hamner, & Prewitt, 1997). Because they are nocturnal animals, they are particularly interesting subjects for analyzing how path integration mechanisms relying on kinesthetic cues are used in the absence of any visual cues.

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METHOD

Estimation of Orientation Angle (Experiments 1–3)

Experimental Set-Up

To understand and explain the fidelity of individual cockroaches to a rest site, we investigated their homing mechanisms. Larvae were chosen for testing, because they feed more often and more regularly than adults involved in the reproductive cycle. Previous results showed that two processes are used by cockroaches to return to their shelter. First, they can use path integration with kinesthetic cues efficiently as soon as they hatch. No improvement of their orientation capacities and no experience effects could be observed with age. Second, they are able to learn visual landmarks that they memorize within the first 3 days of their life (Dabouineau & Rivault, 1995; Rivault & Dabouineau, 1996).

Under our experimental conditions, cockroach larvae were free to navigate from their shelter to a food source. While they were on a food source, we used their natural aptitude to escape toward their shelter after a disturbance to analyze their navigational performance. In dim red light, a shake plus a quick 120° rotation of the food dish distorted and rendered kinesthetic cues inaccurate (Dabouineau & Rivault, 1994) in such a way that they were no longer able to head correctly toward their shelter.

The aim of this paper was (1) to investigate how cockroaches use path integration mechanisms to estimate both components of navigation, orientation angle and return distance, and (2) to demonstrate that they could orient correctly within their home range with the help of only path integration with kinesthetic cues. To this end, in Experiments 1, 2, and 3, cockroach capacities to orientate in complete darkness were tested after the animals had been displaced in their environment, so that information gathered on the outbound journey was no longer exact and no longer oriented them in the right shelter direction. Second, in Experiment 4, cockroach capacities to estimate the distance they needed to travel to reach their shelter were investigated, again in complete darkness. A detailed analysis of the pattern of return paths was undertaken, and the results were compared with aspects that are invariant across species and tied to middle-scale and small-scale navigation constraints.

This experimental set-up was designed to test estimation of orientation angle when the insects left the food dish. They were housed in plastic test boxes ($29 \times 28 \times 8$ cm) without lids. An electric barrier around the top of the box prevented the cockroaches from escaping. One shelter, a black cardboard box ($4 \times 2 \times 1$ cm) with a small entrance on its lower side situated so that its entrance could not be seen from the center of the test box, was placed on the middle of a vertical side of the box. A water source (a soaked piece of cotton wool) was placed near the side opposite the shelter. Food (a piece of bread) was stuck onto a small round plastic dish (3 cm in diameter) in the center of the test box (Figure 1a). The feeding dish was fixed on a bolt that went through a hole in the middle of the test box and through the table, in such a way that the feeding dish could be shaken or turned or both from under the table by manipulating the bolt. Rotation angles of the bolt were controlled with a perpendicular axis through it that hit stoppers placed under the table when the bolt was rotated by hand (Figure 1b).

A series of eight test boxes was placed in the experimental room under controlled temperature (25°C) and light (12:12-h light:dark photoperiod) conditions. A high-sensitivity camera (CCD Ikegami, 0.01 lux) with a zoom and an LED infrared projector was placed on a rail above the test boxes. The camera could be moved along the rail, focusing on each test box in turn. Thus, the camera always gave a picture of the whole test box from the same angle. The infrared projector made it possible to film in complete darkness, so that nocturnal cockroaches were not bothered by any light sources.

Subjects

All the subjects in one test box hatched from the same ootheca, placed in the shelter the day before hatching (Tanaka, 1976). Tests were performed in the middle of the first instar, when the larvae were 3 days old (Dabouineau & Rivault, 1988). Each box was used only once, so that individual larvae were not tested several times. Tests were replicated, as described in detail by Rivault and Dabouineau (1996), until a sufficient number of larvae had been tested under each experimental condition.

Tests

A test measured the escape direction of the larvae from the food dish following a disturbance. The predicted escape direction was the shelter, which was set at 90° (Figure 1a). Paths were filmed and recorded with a S-VHS JVC magnetoscope. The orientation angles

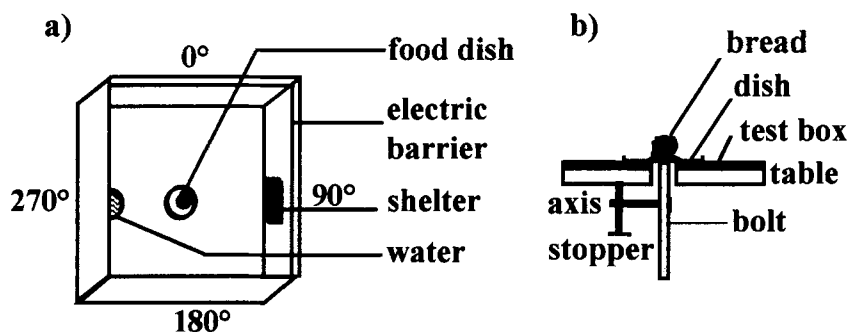


Figure 1. Experimental set-up to study escape angle direction in cockroach larvae: (a) plan view of test box; (b) details of the food dish and attached bolt used to shake and to move the dish from under the table.

of the larvae escaping from the feeding dish were measured when they reached the edge of a circle 12 cm in radius. Directions were measured in degrees. All tests were performed during the first part of the cockroaches' activity period—that is, the night phase of the light:dark cycle, when several larvae had nearly finished feeding.

Two types of disturbance could be applied to the food dish by the same experienced investigator, with the help of the bolt placed through the table. The first type of disturbance was a translation movement without rotation, called a shake. The shake made the larvae escape toward their shelter (Dabouineau & Rivault, 1994) but did not interfere with orientation performance. This disturbance did not affect any memorized cues, either idiothetic or allothetic. The second type of disturbance was a rotation of a given angle, followed by a shake. The rotation had to be performed at a constant speed, neither too rapid, because that would induce loss of path integration information gathered during the outward trip (Dabouineau & Ri-

vault, 1994), nor too slow, because larvae would then leave the feeding dish before the end of the rotation and that data would have to be discarded. The rotation angle was 110° counterclockwise.

Three series of tests were performed.

In Experiment 1 (Figure 2a), our aim was to verify that first instar larvae were able to return to their shelter in complete darkness, without any visual cues. The disturbance was a shake. The expected escape direction, given undisturbed orientation, was 90°.

In Experiment 2 (Figure 2a), our aim was to verify that a rotation did not stress the larvae unduly, so that they would lose their capacity to return to their shelter. The disturbance was a 110° counterclockwise rotation, followed by a shake. The tests were performed during the night phase but in the presence of a dim nondirectional light (3.8 W/m²), which allowed the larvae to use landmarks to reach their shelter. The expected escape direction, given undisturbed orientation, was 90°.

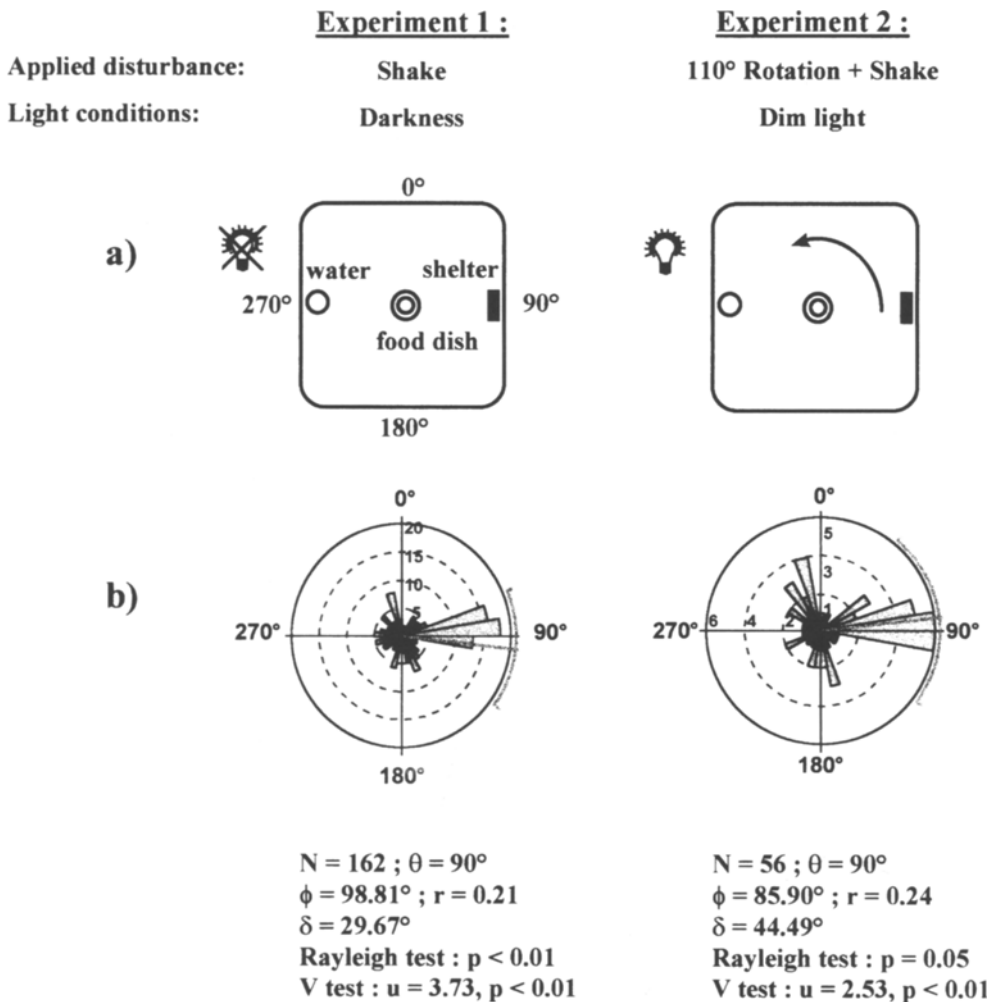


Figure 2. Experiments 1 and 2: (a) Diagram of experimental procedure. In Experiment 1, applied disturbance was a shake in complete darkness. In Experiment 2, it was a 110° counterclockwise rotation, followed by a shake in dim white light. (b) Distribution of angular direction chosen by larvae after disturbance. Length of histogram bars referred to the number of larvae in 10° classes. Statistical analyses of data were obtained by using Oriana software (Kovach Computing System). Angle of mean vector and angular deviation are indicated in gray. *N*, number of larvae; θ , expected escape angle; ϕ , mean escape orientation angle; *r*, mean vector length; δ , angular deviation; *p*, significance level of Rayleigh test and V test; *u*, calculated value of V test.

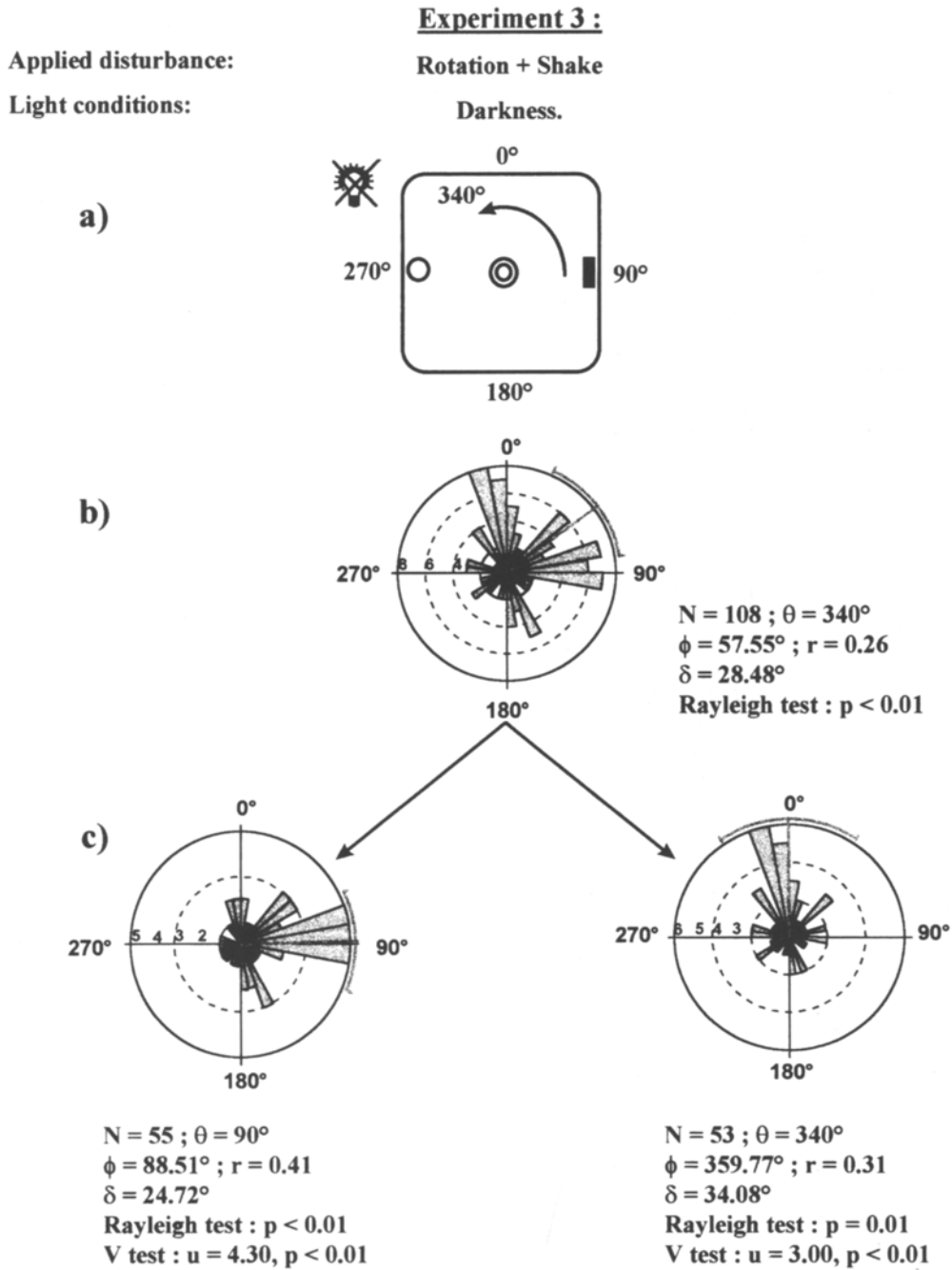


Figure 3. Experiment 3: (a) Diagram of experimental procedure. Applied disturbance was a 110° counterclockwise rotation, followed by a shake in complete darkness. (b) Distribution of angular direction chosen by larvae after disturbance. (c) Angular directions, divided into two subsamples. Left sample, larvae orienting toward 90°. Right sample, larvae orienting toward 340°. *N*, number of larvae; θ , expected escape angle; ϕ , mean escape orientation angle; *r*, mean vector length; δ , angular deviation; *p*, significance level of Rayleigh test and V test; *u*, calculated value of V test.

In Experiment 3 (Figure 3a), our aim was to demonstrate that the larvae used kinesthetic information, gathered during their outward trip, to return to their shelter in complete darkness. When the position of the larvae was modified in relation to their shelter without modifying information gathered during the outward trip—that is, they were

rotated 110° passively—it was hypothesized that they would head toward a direction that included the 110° of the passive rotation. The applied disturbance was a 110° counterclockwise rotation, followed by a shake. This experiment was performed in complete darkness. The expected escape direction, given undisturbed orientation, was 340°.

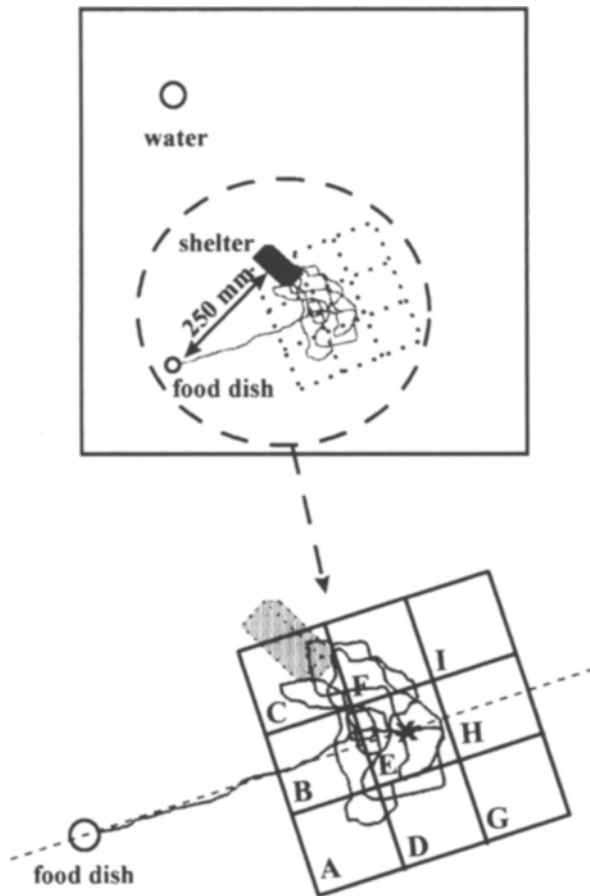


Figure 4. Experimental set-up to study distance estimation (Experiment 4). View of the 1-m² arena, with positions of water source, food dish, and shelter before the test. A test consisted of taking away the shelter and shaking the food dish. In the dotted circle is shown a recorded escape path (gray) with the grid used to analyze its components. The middle of the grid is centered on the arrest position (X) of the escape path and oriented along an axis made by the food dish and the arrest position (dashed line). The shaded rectangle indicates the position of the shelter. Grid units are lettered from A to I.

Estimation of Distance (Experiment 4)

Experimental Set-Up

The set-up used in Experiments 1–3 was not large enough to allow us to test distance estimation when the insects left the food dish and returned to their shelter. A larger arena was designed. Distance estimation capacities in cockroaches was tested in a large (1 m²) glass arena equipped with an electric barrier. A cardboard shelter (10 × 3 × 3 cm) was now placed in the center of the arena, and a food dish was placed in one corner of the arena, 250 mm from the shelter. Water was placed in another corner (Figure 4). Thin wires were fixed on top of the shelter and on the feeding dish to facilitate handling by the experimenter in total darkness. The arena was covered with clean paper every day just before lights off, so that no olfactory marks could interfere with path integration mechanisms when the subjects were tested.

Escape paths were video recorded with a high-sensitivity camera (Philips CCD camera) and an LED infrared projector in complete darkness. The lens of the camera allowed us to record the escape

path over the whole surface of the arena. Paths were analyzed, using image-processing software (written by J. P. Richard, CNRS UMR 6552). This program plots paths and computes durations and lengths of different parts of paths.

Subjects

The subjects used to test distance estimation capacities were 4th and 5th instar larvae. We used older larvae for technical reasons. The ratio between the size of the tested insect and the surface of the arena had to be large enough for the image processor to record the insect movements. This change was made possible because no improvement in orientation capacities owing either to variations in path integration mechanisms or to experience with age were observed (Dabouineau & Rivault, 1995). One hundred and fifty larvae were placed in the arena a few days before the test, so that they could habituate to their environment.

Tests

The aim of the tests in Experiment 4 was to analyze the capacities of cockroaches to estimate the distance from the feeding dish to their shelter, using kinesthetic cues collected during the outward trip. The test measured their ability to locate the site of their shelter after it had been removed, sometime between their outward trip and their return trip.

A test was made when at least 5 larvae were on the food dish. Before the disturbance, the shelter, with the animals still in it, was carefully lifted out of the arena with the help of the wire. Then, the feeding dish was shaken by using the wire without rotation (see details above). The purpose of this study was to analyze distance estimation, not orientation abilities. Before replacing the shelter in the arena, all the larvae that had been tested were caught and removed, so that each individual was tested only once.

Data Analysis

Estimation of Direction (Experiments 1–3)

Escape directions were measured in angles, ranging from 0° to 360°. Data and graphical presentations were analyzed as circular variables, according to Batschelet (1981), using Oriana software programs (Kovach Computing System). The shelter direction was set at 90°. Applying vector algebra, we calculated the mean vector with its two polar coordinates, r (length ranging from 0 to 1) and Φ (mean orientation angle), and its confidence interval δ for each set of data. Significance was estimated by using Rayleigh and the V tests, which are goodness-of-fit tests for randomness.

The hypothesis tested was that cockroaches would be able to find their shelter, against the null hypothesis that they would not. If the observed distribution of data was unimodal, we reasoned, the significance of the Rayleigh tests and the V tests would prove not only one-sidedness but also a concentration of directions around the mean direction, which could be called the preferred direction.

Estimation of Distance (Experiment 4)

Each path was analyzed for 36 sec after the food dish had been left. Several characteristics of paths were analyzed. Each path was characterized by a linear oriented-to-the-goal trajectory, an arrest position at the end of this oriented trajectory, and a second part with a systematic search path centered around this arrest position.

The first part of the path was characterized by its orientation angle, distance traveled from the food dish to the arrest position, and speed of the insect during this part of the trajectory. The second part of the trajectory was analyzed by measuring the length of the path step by step through a grid centered on the arrest position and oriented along an axis made by the feeding dish and the arrest position. The grid was composed of nine 100 cm² units (Figure 4). Further analysis indicated the position of the insect in relation to the arrest position every 2 sec, as well as its mean speed for this part of the path.

RESULTS

Estimation of Direction (Experiments 1–3)

Experiment 1 : Shake in Complete Darkness (Figure 2b)

Experiment 1 was a basic control under our experimental conditions. After a shake, the larvae escaped from the food dish toward the shelter. The only cues they could use for their return trip in complete darkness were kinesithetic cues. The larvae did not orient uniformly in the test box (Rayleigh test, $p < .01$). The confidence interval of the mean escape direction ($\Phi \pm \delta = 98.8^\circ \pm 29.7^\circ$) contained the 90° theoretical escape direction given by the shelter position. The V test was significant ($u = 3.73$, $p < .01$). These results meant that the majority of larvae oriented toward their shelter. Therefore, cockroach larvae were able to return to their shelter in the absence of visual cues. We hypothesize that they use cues gathered by path integration mechanisms during their outward journey to find their way back to their shelter.

Experiment 2: 110° Rotation in Dim White Light (Figure 2b)

Experiment 2 was designed to confirm previous results (Dabouineau & Rivault, 1994) under our ongoing experimental conditions. Our data showed that rotation did not induce a loss of return capacities to the shelter in dim white light. Larvae escaped in a preferred direction because the distribution of escape directions after rotation plus shake was not uniform (Rayleigh test, $p < .01$). The V test ($p < .01$) showed that angular values were grouped significantly around 90° , as this theoretical escape direction was included in the confidence interval of the mean escape angle. This rotation did not induce nonoriented escape in the test box; the cockroaches were able to return to their shelter correctly, using visual cues. The stress induced by the rotation was strong enough to induce the expected escape behavior.

Experiment 3: 110° Rotation in Complete Darkness (Figure 3b)

This experiment aimed to verify that, after a rotation in complete darkness, the larvae were able to orient in a hypothetical shelter direction that included the passive rotation angle. After an 110° counterclockwise rotation in total darkness, the larvae did not escape in all directions; the Rayleigh test was significant ($p < .01$), indicating that the distribution of escape directions was not uniform. However, neither 340° , the theoretical position of the shelter after rotation, nor 90° , the real position of the shelter, were included in the confidence interval of the calculated mean escape angle. This distribution appeared bimodal, with one peak approximately at 90° and another at 340° . Since there is no standard method to disentangle a bimodal sample, we adhered to an ad hoc procedure described by Batschelet (1981). We separated the group frequencies by trial and error in such a way that two unimodal and approximately symmetrical samples

resulted. The data were separated between two groups, one subsample containing animals orienting toward 90° and the other subsample containing larvae orienting toward 340° (Figure 3c).

We hypothesized that some larvae took into account the passive rotation in the calculus of their orientation angle toward the shelter, still orienting toward 90° , whereas others did not and oriented toward 340° . Larvae in the first subsample oriented significantly toward 90° (Figure 3c); the Rayleigh and V tests were significant, and 90° was included in the confidence interval of the mean vector angle. These larvae appeared to have compensated for the rotation of the feeding dish before choosing their escape direction toward the shelter and to have integrated the rotation in the calculus of their home vector direction. The larvae in the second subsample (Figure 3c) oriented toward 340° , which was included in the confidence interval of the angle of the mean vector. It seemed that these larvae did not perceive the rotation and behaved as though they had not been moved. During their outbound journey, larvae measure and integrate rotations and distances traveled so that, at any moment, they know their position in relation to their shelter. In the second subsample, they ignored the passive rotation and oriented in the direction in which the shelter would have been if they had not been rotated—that is, the direction indicated by their return vector, calculated by path integration mechanisms. The response of the larvae in this second subsample proves that cockroaches did use idiothetic cues, taken during their outward trip, to integrate their return path in the absence of any other type of cues—in particular, visual cues.

Estimation of Distance (Experiment 4)

The success of a return path depends of two variables, the orientation angle and the distance estimation of the goal. As we have seen above, cockroach larvae are able to orient in the correct direction in complete darkness, using path integration cues. These experiments aimed to verify that they were also able to estimate the distance from the goal under the same conditions.

Two types of paths were observed, in relation to the presence or absence of an arrest during escape (Table 1).

Table 1
Speed and Duration of Paths With and Without an Arrest

Paths	Number of Paths	Speed (mm/sec)		Duration (sec)	
		<i>M</i>	<i>SE</i>	<i>M</i>	<i>SE</i>
Without arrest	36	162.6	9.2	6.0	0.8
With arrest	55	55.1	4.3		
Before arrest		153.4	7.3	2.7	0.1
Arrest position				1.0	0.05
Underestimation	5				
Good estimation	17				
Overestimation	33				
After arrest		43.5	3.1	35.8	3.1

Note—Shelter position was underestimated when path lengths were less than 250 mm, correctly estimated for lengths between 250 and 300 mm, and overestimated for lengths above 300 mm.

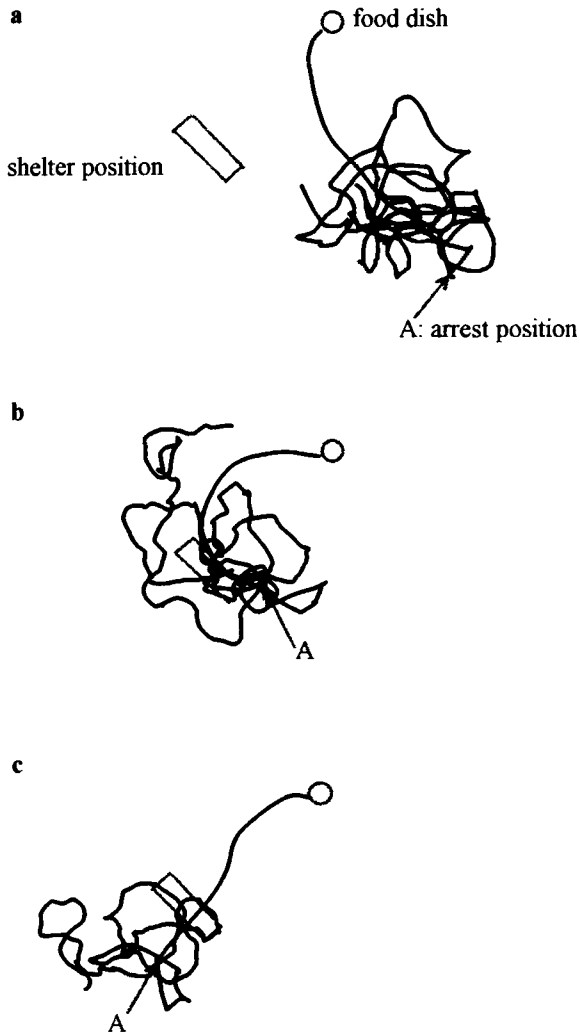


Figure 5. Examples of three escape paths (a, b, and c) in Experiment 4. Gray circles indicate the food dish, departure of the return path. Gray arrows indicate the arrest position, and gray rectangles indicate the shelter. The paths lasted between 80 and 91 sec and were between 254 and 425 cm long.

The first type of path (60% of the paths) was characterized by a nearly linear oriented-to-the-goal trajectory (mean duration = 2.7 ± 0.1 sec, speed = 153.44 ± 7.3 mm/sec), an arrest of this oriented trajectory (mean duration = 1 ± 0.05 sec), and a final long-lasting search (35.8 ± 3.1 sec) at a much slower speed (43.5 ± 3.1 mm/sec; Figure 5). The second type of path (the remaining 40%) did not present an arrest and presented no changes in search strategy. The mean speed of cockroaches that did not pause during their escape was significantly higher than that of cockroaches that paused (t test $> 5.10^6$, $p < .001$). These cockroaches were highly stressed and ran away until they reached the arena border (83%). After they reached the border of the arena, they tended to follow it (Darchen, 1954). Therefore, these larvae were not included in further analyses.

To make sure that the clean paper bore no olfactive trace of the shelter that could induce arrest, we compared the number of paths with and without an arrest in relation to whether the animal did or did not pass over the site previously occupied by the shelter. Passing over the shelter site did not significantly induce an arrest [$\chi^2(1) = 1.21$, $p > .05$, n.s.]. Therefore, we can conclude that the clean paper presented no odor cues indicating the shelter site. The only cues that insects could use in this experiment were path integration cues.

We hypothesized that the arrest position observed in the first type of path was induced by the absence of the shelter where the animals expected to find it. The arrest, which lasted a relatively long time, as compared with the first part of the trajectory, was followed by a complete change in behavior. Mean speed was higher before the arrest than after it ($t > 5.10^6$, $p < .001$; Table 1). Therefore, the length of the escape path to the arrest position was considered to represent the distance cockroaches estimated to be necessary to reach their shelter. Path lengths between 250 and 300 mm were considered to be good estimations of distance to shelter, depending on whether the distance from the food dish to the nearest or the farthest edge of the shelter was considered; shorter paths were considered to be underestimations, and longer paths were considered to be overestimations.

Very few (9%) of the cockroaches that arrested appeared to underestimate the distance to the shelter (Table 1). These animals might have been more highly motivated to feed than to return to their shelter after the disturbance, so that they stopped very soon, in order to return immediately to the feeding dish. Approximately one third of the animals estimated the distance to their shelter correctly. However, there was a significant tendency for cockroaches (60%) to overestimate that distance [$\chi^2(2) = 21.33$, $p < .01$].

Distance and Angle Errors

Our results showed that both measures, orientation and distance, can present errors in estimation. An individual cockroach can estimate one parameter wrongly and the other correctly and the reverse.

The accuracy of distance estimation in cockroaches (Experiment 4), was not correlated with the accuracy of direction estimated on leaving the feeding dish (correlation coefficient = .05, n.s., $N = 55$).

Although both parameters (distance and direction) are estimated by kinesthetic cues and integrated into the home vector, the accuracy of each measure seemed to be independent.

Systematic Search Strategy

We analyzed the systematic search paths of the larvae following arrest (Experiment 4).

End of Escape Path

Escape paths had highly variable durations. The ends of the 55 recorded paths for which arrests were observed

Table 2
Mean Length (in Millimeters, With Standard Errors) of Path Portion in Grid Units Described in Figure 4

Orientation Around the Arrest Position	Grid Units	Length	
		<i>M</i>	<i>SE</i>
Upstream units	A	49.0	21.0
	B	130.3	29.4
	C	44.5	18.7
Left unit	D	60.4	19.6
Central unit	E	202.0	33.3
Right unit	F	90.6	25.5
	G	19.9	8.7
Downstream units	H	77.8	21.9
	I	30.4	11.8

could reflect the fact that the escaping cockroach had either reached the food dish (35%) and resumed its interrupted food intake, hit the border of the arena (42%) and walked along it, or encountered another larva (5%) and deviated its path, or that the recording was interrupted (18%). Therefore, in most cases, environmental heterogeneities interrupted the search.

Systematic Search Path Patterns

It seemed that the arrest marked a behavioral modification, suggesting that cockroaches passed from an oriented escape to a search for the shelter. The analysis of the final part of the return path after the arrest indicated that the search was made at constant speed. Twenty-five of 55 recorded paths with an arrest were analyzed in detail during the first 36 sec with a grid centered on the arrest position and oriented along an axis made by the food dish and the arrest. The other paths were discarded from this analysis, because they were too short. The total portion of path in a grid unit varied in relation to the position of the unit on the grid [in an analysis of variance (ANOVA), $F(8,216) = 6.55$, $p < .001$; Table 2]. The longest portions of path were observed in grid unit E (central part of the grid directly around the arrest position; Figure 4). Lengths of portions in upstream grid units A, B, and C were significantly longer than those in downstream grid units G, H, and I [ANOVA, $F(5,144) = 4.13$, $p = .002$]. No significant differences in portion lengths were found between left grid units A, D, and G and right grid units C, F, and I [ANOVA, $F(5,144) = 1.81$, $p = .115$]. Therefore, after the arrest, search was not random but centered around the arrest position, which was considered by the insects to be the position of the shelter. Furthermore, search was more intense in grid units located upstream from the arrest than in downstream grid units but presented no left or right tendency.

As cockroaches had a tendency to direct the most important part of their systematic search around their arrest position, the spatiotemporal pattern of the search path was studied, using paths lasting more than 80 sec (Figures 5 and 6). The distance between each position of a larva and its arrest position in relation of time was measured. Although only six search paths were long enough

to be analyzed this way, cockroaches seemed to loop back and forth around their arrest position, increasing the size of their loops. Therefore, the shape of cockroach search paths could be compared with search behavior exhibited by desert isopods (Hoffman, 1983a, 1983b) and desert ants (Wehner & Srinivasan, 1981), some parts of which were compared with spirals. Because of the small number of long paths for cockroaches and the different methods used by the authors, it is difficult to make quantitative comparisons between species.

DISCUSSION

Our study provides strong evidence that cockroaches are capable of assessing the characteristics of an outward trip to a feeding place in order to estimate the direction as well as the distance for a return to the shelter from which they started, relying only on path integration with kinesthetic cues. Detailed analysis of cockroach return trips revealed some interesting similarities with other arthropod path integration trajectories.

A demonstration that ants rely on path integration mechanisms to navigate was made with displacement experiments. Ants displaced from their starting position and released at a new one kept their direction and distance of travel unchanged, as though they were unaware of having been displaced (Wehner & Wehner, 1986). The passive rotation applied in our experiments was designed for the same purpose. Our data reflect the fact that cockroaches are very susceptible to any passive movement and, thus, very difficult to manipulate. Whereas some individuals that were submitted to a passive rotation took a wrong orientation angle for their return trip, others took the shelter orientation. The first ones were not able to modify the orientation angle of their home vector and headed in the wrong direction. The others integrated the passive rotation in their angular calculus and took the right shelter direction.

Obviously, the rotation of the food dish was not perceived the same way by all the larvae and, consequently, was integrated differently in the home vector. Nevertheless, we are sure, at least, that larvae heading toward 340° used path integration mechanisms during their return trip. When the stress was applied to the food dish, two types of behavioral answers were observed, because all the larvae either were not exactly in the same position on the food dish or did not have the same behavioral motivation. Some of them were feeding, whereas others were not and were still exploring the food dish. Feeding cockroaches might have been less sensitive to surrounding stimuli and did not perceive the rotation, whereas non-feeding cockroaches were more sensitive and included the rotation angle in their return vector calculus. At present, our camera does not allow us to separate these two kinds of subjects.

The analysis of return paths revealed that cockroaches were also able to estimate the distance from the shelter—the second component of the home vector. An arrest end-

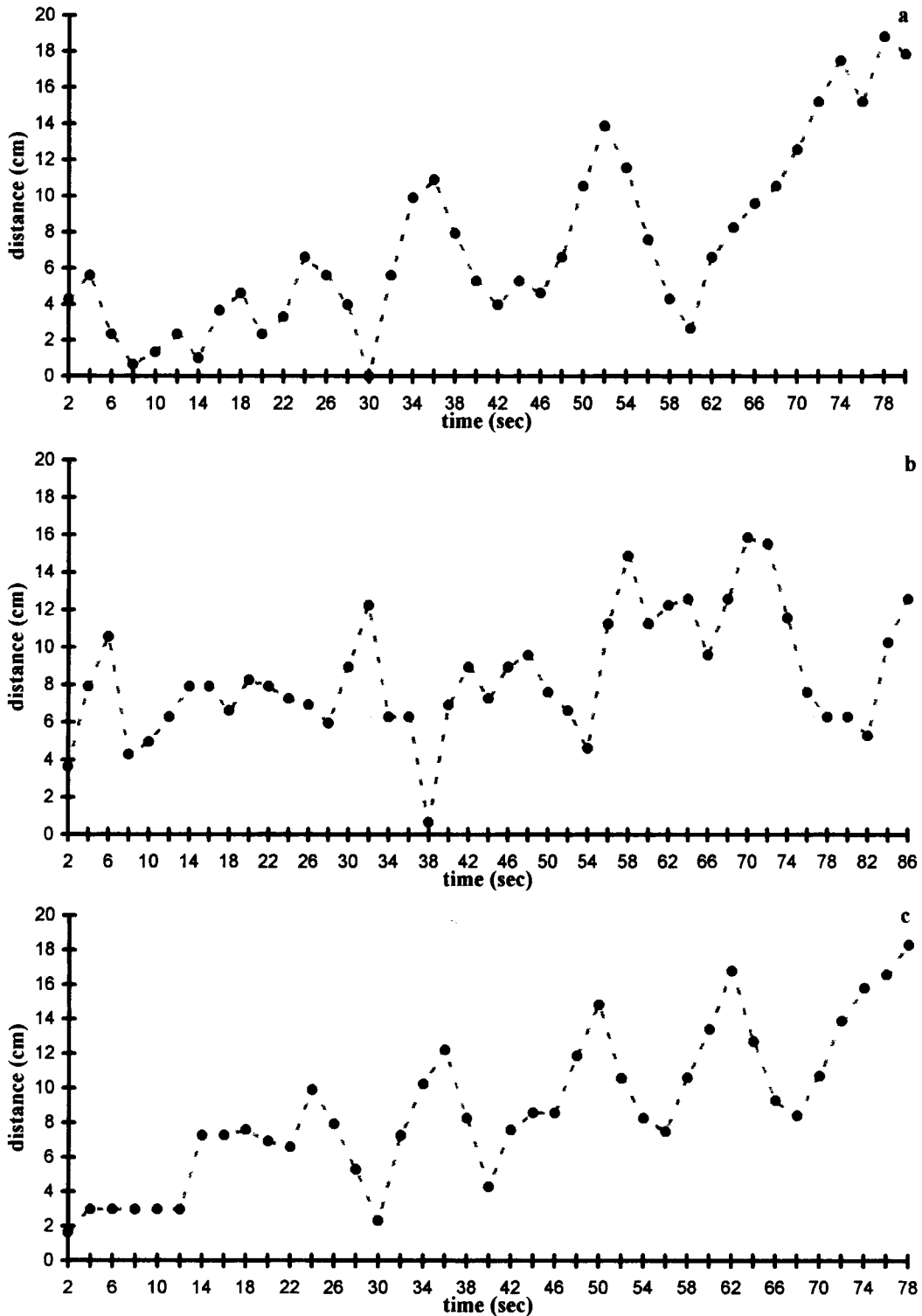


Figure 6. The distance of an individual's position from the arrest position in Experiment 4 is plotted every 2 sec. The curves in panels a, b, and c correspond to the three paths given in Figure 5.

ing the oriented escape path allowed us to deduce that the length of the path between the food dish and the arrest position corresponded to the food dish–shelter distance estimated by the cockroach. This position also in-

dicated that the home vector was back to zero (Wehner et al., 1996). Many arthropods seem able to estimate the distance between their position and their shelter and then to develop an adaptive search strategy, in the absence of

their shelter, to compensate for inaccurate direction estimations (Collett, Baron, & Sellen, 1996; Hoffmann, 1983a, 1983b, 1984; Seyfarth et al., 1982; Wehner, Harkness, & Schmid-Mempel, 1983; Wehner & Srinivasan, 1981). In diurnal insects such as bees, estimation of distance is measured by self-induced retinal image flow (Esch & Burns, 1996; Ronacher & Wehner, 1995; Srinivasan, Zhang, Lehrer, & Collett, 1996) and not on the basis of energy expenditure (Schäfer & Wehner, 1993). In ants, step length is constant at a given walking speed (Zollikofer, 1994), and walking speed is constant for a given trip (Wehner & Srinivasan, 1981), so that distance traveled is related to the number of steps. Distance estimation using kinesthetic cues has already been evidenced in isopods (Hoffman, 1984) and in spiders (Seyfarth & Barth, 1972), where exoskeletal sensors work as strain gauges (Zill & Seyfarth, 1996). In the present experiments, no external cues (i.e., visual cues) were available for navigation, and cockroaches relied exclusively on directional information from their own movements, provided by campaniform sensillum located on different parts of the legs (Zill & Seyfarth, 1996).

In response to feedback indicating that they had missed their target (when the shelter failed to be at the arrest position), cockroaches started a nonrandom systematic search path directed mainly around the arrest position. Cockroaches looped regularly back and forth around the arrest position and increased the size of their loops with time. If larvae do not find their target exactly where they estimate the target should be, they have no way of determining the nature of the error. Our results can be compared with search behavior exhibited by desert isopods (Hoffman, 1983a, 1983b) or desert ants (Müller & Wehner, 1994; Wehner & Srinivasan, 1981). On the basis of computer simulations, these authors concluded that invertebrates walk along a spiral trajectory interrupted by several walks toward the arrest position. Animals continually update their home vector, taking the start of the search as the reference position. When an animal nears its starting position, its home vector is reset at zero (or reduced); consequently, computational errors inherent to path integration processes, increased by systematic turns, are reduced (Wehner et al., 1996). Each time the home vector is reset, animals start a new loop with a larger turning angle, so as to move in a spiral. All the experimental components of cockroach search paths (Figure 6) fit this definition, even if cockroach search paths are much shorter and last for less of a time than desert ant paths, which can measure up to 1 km (Wehner & Srinivasan, 1981). Cockroaches rarely exhibit such long search paths, because their home range is smaller (Rivault, 1990). Furthermore, their natural environment potentially contains many objects that can be used as beacons, and direct contact with any object is sufficient to stop a search. Furthermore, in their familiar environment, they encounter a variety of tactile, olfactory, and visual cues.

Our results showed that both measures, orientation and distance, presented errors in estimation and that the

accuracy of each measure was independent. In bees, distance and direction are encoded in such a way that the two parameters interact at the level at which visual signals become linked to trajectory commands. Length and direction of trajectories are not treated separately (Collett et al., 1996). Further experiments will be necessary to try to understand why estimation errors involving these two parameters are not correlated in cockroaches and why these errors seem to indicate that they are represented independently. Systematic errors in orientation have been reported in nearly all species using path integration mechanisms (Görner & Claas, 1985; Maurer & Séguinot, 1995; Müller & Wehner, 1988; Wehner & Srinivasan, 1981). The inaccuracy of estimations by idiothetic cues suggests that nocturnal animals rely on several other kinds of cues to improve their navigation performance, such as olfactory (Benhamou, Sauve, & Bovet, 1990) and visual (Rivault & Dabouineau, 1996) cues.

Our experiments indicated that cockroaches used path integration to navigate in complete darkness, in the absence of any other cues. They were able to return to their shelter along an integrated path whose orientation and estimated length were defined by the home vector. This return path was based on idiothetic cues gathered during the outward trip. While foraging, they measured angles turned and distances covered and integrated these data into a continually updated home vector. During homing, the length of the home vector decreased. When a cockroach reached a place that it estimated to be its shelter position because its home vector had reached zero, the cockroach indicated that by a marked arrest, similar to arrests described in many invertebrate species. If it had not reached the shelter because of errors in the path integration system, it started a systematic search around this arrest position. The efficiency of these navigational abilities is based on a minimalist cognitive architecture (Dyer, 1996) relying on path integration cues. Some other cues related to experience and memorization of spatial relationships between landmarks may be added to this minimal frame to improve their abilities. This search strategy is considered to be an ubiquitous trait in invertebrates (Wehner & Srinivasan, 1981). Inasmuch as it has been described in all types of social organizations, from solitary animals (spiders), to family groups (isopod crustaceans), to social congregations (cockroaches), to eusocial insects (bees and ants), this search strategy could be considered to be a primitive trait in invertebrates.

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