Journal of Chemical Ecology, Vol. 15, No. 1, 1989

COUNTERTURNS INITIATED BY DECREASE IN RATE OF INCREASE OF CONCENTRATION

Possible Mechanism of Chemotaxis by Walking Female *Ips paraconfusus* Bark Beetles

R. PATRICK AKERS[1]

Department of Entomological Sciences, University of California, Berkeley, California.

(Received June 8, 1987; accepted November 5, 1987)

Abstract—The position of beetles were marked at 1-sec intervals after they were released in still air 16–18 cm from point sources of pheromone. Characteristics of the tracks were quantified and compared to those that might be produced by counterturning schemakinesis, tropotaxis, klinotaxis, zigzagging, look-and-leap, or steepest-ascent schemakinesis mechanisms. The beetles' movements were highly irregular, but they turned almost continually and never fixed on a heading near 0° (=straight towards the source). Turn angle sizes increased slightly with absolute size of heading but had the opposite sign, thus compensating slightly for heading. Their distribution was centered about 0° and was unimodal. Heading decreased gradually as the source was neared, but the decrease became steeper within 1-5 cm of the source. Histograms showed that the maximum headings between occurrences when the beetle was headed directly towards the source (0°) were centered around 0° and most of them were less than 90°. However, maximum headings between 90° and 180° were not uncommon. Turn radius decreased as the source was neared. The counterturning mechanism was the most consistent with these observations. An analysis of rate of change of concentration with respect to heading and distance to the source further demonstrated that the counterturning mechanism could explain the form of the decrease in heading as the source was neared, if the major cue used to initiate counterturns was a decrease in the rate of increase of concentration. The tropotaxis could not recreate the form of the decrease, under any form of stimulus processing.

Key Words—*Ips paraconfusus*, Coleoptera, Scolytidae, bark beetles, olfaction, orientation, counterturning, chemotaxis, taxis, pheromones, tropotaxis, schemakinesis.

---

[1] Present address: Worcester Foundation for Experimental Biology, 222 Maple Ave., Shrewsbury, Massachusetts 01545.

INTRODUCTION

Ips paraconfusus Lanier (Coleoptera: Scolytidae) has three compounds in its pheromone, which it uses to orient with respect to mates, competitors, and hosts (Silverstein et al., 1966; Wood et al., 1967). The analyses described here arose from experiments undertaken to develop a behavioral assay for olfactory quality discrimination among the components of the pheromone (Akers, 1985; Akers and Wood, 1987b). Chemotaxis was one behavior used as the basis for an assay. The responses in this assay were striking (Akers, 1985; Akers and Wood, 1987a). From a distance of 16–18 cm, approximately 80–90% of all beetles located sources of 0.1–1.0 mg of pheromone, guided by odor alone. I became interested in the mechanisms underlying the taxis, because of its apparent efficiency. A more complete description of the mechanism was not necessary to use the assay as an indicator of olfactory quality, but it would aid in limiting the possible neural mechanisms that could be involved in orientation.

Previous work established the hypothesis that the initiation of chemotaxis was essentially an all-or-none phenomenon (Akers, 1985; Akers and Wood, 1987a). The behavior of beetles that did and did not reach the source was qualitatively different, while the behavior of beetles within either of these groups was very similar, even though the beetles were exposed to dosages differing by several orders of magnitude. Thus, the major influence of increasing pheromone dosage was to increase the probability that a beetle would initiate orientation.

The mechanisms by which an orienting beetle reaches the odor source are explored in this paper. Its premise is that orientation based on different sources of information will produce tracks that differ in form. Quantitative analyses were designed to describe various aspects of track form. The predicted effect of several possible orientation mechanisms on each analysis was then compared to the observed results to identify any particular mechanism that might be consistent with the observations. The analysis indicated two major hypotheses concerning the mechanism of orientation. First, an orienting beetle locates the source by turning in one direction until it detects a critical sensory cue, at which time it initiates a turn in the opposite direction. This mechanism is termed a counterturning schemakinesis (Kennedy, 1986), or counterturning, for short. Second, if counterturning is the mechanism, the major cue used to initiate a counterturn appears to be a decrease in the rate of increase of concentration.

METHODS AND MATERIALS

The compounds used as stimuli, the observation chamber, the recording procedures, the handling of the experimental animals, the experimental design, and some of the analytical methods for orientation data have all been described previously (Akers and Wood, 1989a). The basic experimental design was a dosage series of a 1 : 1 : 1 blend of the three pheromonal compounds, ipsenol (Ip), ipsdienol (Id), and *cis*-verbenol (cV). The dosages differed by powers of ten, running from 10^{-4} to 1 mg, and were dissolved in 0.1 ml pentane. The series was run with diffusion periods of 30 and 60 min in separate experiments.

The position of each beetle was marked at 1-sec intervals after it was released in still air 16–18 cm from a point source of pheromone. The angle the beetle turned at each point on its track was measured. The turn angle was defined as the angle between the direction from the current point had the beetle continued walking straight ahead along the line from the previous to the current point on the track, and the direction from the current to the next point. Zero degrees was defined as straight ahead. A heading was also measured at each point on a track. The heading is the direction an animal takes with respect to the pheromone source, at any given point on its track. It was defined as the angle between the direction towards the source from the current point on the track and the direction from the current point to the next point on the track. Zero degrees was defined as straight towards the source. For "net" angle summaries, left-hand angles were defined as positive. For "gross" angle summaries, the absolute values of the angles were used (Akers and Wood, 1989a). Summaries of walking rate and its variation within a track, net turning rate, gross turning rate and its variation within a track, mean net heading, and gross heading and its variation within a track have been reported elsewhere (Akers, 1985; Akers and Wood, 1989a). Further analyses were needed to identify the probable mechanism of chemotactic orientation. Unless otherwise noted, the following analyses were made on only those beetles in a treatment that reached the source and on control beetles when comparisons with nonorienting beetles seemed appropriate.

Histograms were made of the size of the turn angles, to determine whether their distribution was unimodal or bimodal. A bimodal distribution would have indicated that the beetles had two distinct rates of turning, such as might occur if linear sections of track were interspersed with more rapid turning. A bin size of 10° was chosen for this analysis. The recording procedures were accurate to only 2–5°, and even beetles in control situations had standard deviations of 8–15° in their turn angles (Akers and Wood, 1989a). Any much smaller bin size seemed inappropriate. The results for both the 30- and 60-min diffusion periods were extremely similar. Only the results from the 60-min period experiment are shown for illustration.

The beetles' movements were very irregular or noisy (Figure 7 in Akers and Wood, 1989a). Some orientation mechanisms might be expected to produce noisy tracks, while others would more likely produce more regular oscillatory or patterned movements. Therefore an analysis of the variation of the "overall turn" or "arc" sizes of the swings on a beetle's track was made. A "turn" could mean the turn angle at a particular point on a beetle's track. However, a track is more usually perceived, not as a series of points, but as a series of "arcs" or "swings" or "turns." An arc is usually recognized when a series of turn angles all have the same sign, or at least mostly so, and their signs are opposite to those of the series of turn angles just preceding and following the arc in question. To avoid confusion, the use of "turn" will be avoided, and "turn angle" and "arc" will be used in the above sense.

A program was developed to analyze the number of degrees turned in an arc. It was based upon the following set of criteria, which was intended to filter out variation due to recording procedures and very small turn angles made by the beetles: (1) Each point was considered sequentially and, if its turn angle was of the same sign as the immediately preceding points, it was summed with those points. (2) If the turn angle was of the opposite sign from the preceding points, several different possibilities were evaluated. (2a) If its absolute angle was greater than 10°, it was accepted as initiating a new arc. Ten degrees was chosen because it was about twice the measuring error for a single turn angle (Akers, 1985; Akers and Wood, 1989a) but still less than half the average turn angle even for control beetles. (2b) If the turn angle was less than 10°, the next point on the path was checked. (3a) If the sum of the points was more than 15° and if both points were of the same sign, they were accepted as a new arc. (3b) If a turn angle was not accepted as a new arc, it was summed into the previous arc.

The above algorithm filtered out the very noisy arcs, and its determinations of arcs were generally in accordance with subjective judgments in the sense that, where the program indicated an arc, an arc would be recognized. The standard deviation of the arc sizes within each track was used to probe for regular movements. There was no a priori reason to suppose that every beetle should have a similar mean arc size, i.e., the size of arcs made by a beetle might well have a strong component due to the individual beetle. However, if regular oscillatory or patterned movements were occurring, the arcs of a given beetle should all be of a similar size, and the variation of the arc size should be low for every beetle, regardless of each beetle's particular mean arc size. A consideration of the general heading of the beetle during an arc was also important. Several of the mechanisms might conceivably produce a track that would oscillate regularly back and forth about a heading of 0°. However, only in those in which the basic turn pattern was centrally generated should the regular, oscillatory movements continue regardless of the heading with respect to the source. Mechanisms based on a balance of sensory input ought not generate regular, uniform turns at headings away from 0°. Accordingly, the program also calculated the net heading of each arc. Forty-five degrees was chosen as an arbitrary cutoff for arcs with a heading near 0°, for the purpose of pooling the data.

The maximum absolute heading with respect to the source was determined between occurrences where the heading was 0°. This measured how far away a beetle turned from the source before turning back towards it, and thus gave a measure of the heading at which a beetle initiated its turns back towards the source. If an insect turned beyond 180° or went in a circle, this heading was defined as 180°.

The effects of distance from the source on gross heading were explored graphically and by linear regressions. Similar analyses were done for walking and turning rates (Akers, 1985), but are not shown here. Turn (=arc) radii were not measured directly but were estimated from walking and gross turning rates using the relationship:

$$r_c = (360 \times WR)/(2 \times \pi \times GTR),$$

where r_c = turn radius, WR = walking rate, and GTR = gross turning rate.

The relationship between the gross (absolute) heading of a beetle at a point and the gross turn angle that was subsequently made at that point was estimated by linear regression, to reveal any tendency of the beetle to stabilize on a heading of 0°. Similar regressions were made between the net (actual) heading of a beetle at a point and the net turn angle that was subsequently made at that point (Bell and Tobin, 1981, 1982), to reveal any mechanism where the insect was able to more or less efficiently estimate the direction towards the source.

RESULTS

Frequency histograms of turn angle size showed that the distribution was centered about 0° and that it fell off smoothly and without any intermediate peaks at higher turn angles (Figure 1). The distributions were unimodal, indicating that the beetles apparently did not have two distinct turn angle sizes within the track, such as might occur if tight arcs were interspersed with relatively straight sections.

No consistent pattern in the analysis of overall arc size appeared among the dosages (Table 1), except that the beetles responding to a source consistently turned through more degrees of arc than beetles in blank arenas. The overall coefficients of variation were in the range of 60–90% (calculated from Table 1). This does not seem to be a very low amount of variation, since it would produce an error confidence interval for the arc size at least as large as the mean itself. Coefficients of variation for moths zigzagging in an odor plume appear to be 20–30% (Kuenen and Baker, 1983; Cardé et al., 1984). By contrast, the beetles' movements are highly irregular (examples of trails may be found in Figure 7 of Akers and Wood, 1989a). The variation was similar both when the heading was less than and greater than 45°, although the variation was possibly a bit smaller at headings less than 45°. Low variation at both low

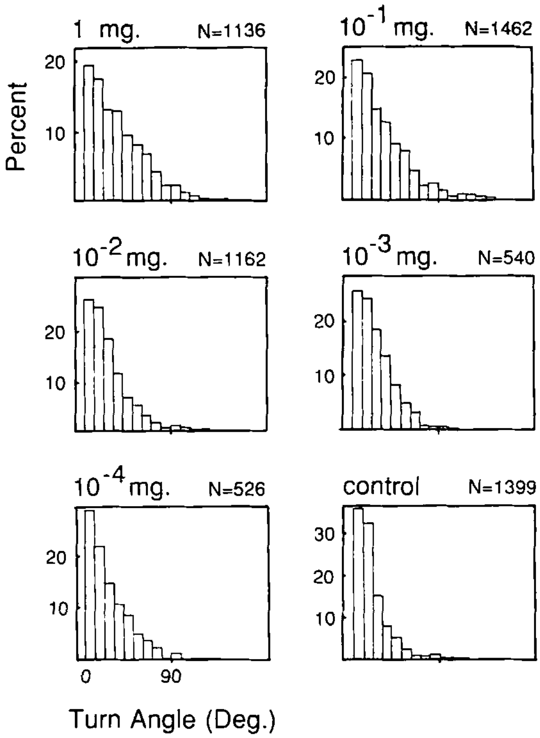


FIG. 1. The number of occurrences of turn angle sizes within each 10° interval in each treatment of the experiment with the 60-min diffusion period. The unimodal distribution suggests there were not two classes of turn angles sizes, such as might have been expected if straight sections were interspersed with bouts of turning. N = total number of turn angles in treatment.

and high headings would have been consistent with regular movements driven by a central pattern generator, while low variation at low headings and high variation at headings farther from the source would have been consistent with regular movements driven by a highly efficient mechanism based on sensory input. High variation at both low and high headings would seem more consistent with mechanisms where the movements are derived from chemosensory input.

In comparing the gross (absolute) heading of a beetle at a point to the absolute turn angle that was subsequently made at that point, the most important result was that the intercepts of the regression lines were always significant and in the range of 20–30° (Table 2). Thus, the beetles continued to have moderate rates of turning even when they were headed almost directly towards the source.

TABLE 1. EFFECTS OF DOSAGE AND HEADING OF ARCS ON ARC SIZE

		All arcs		Mean net headings > 45°		Mean net headings < 45°	
Diffusion period (min)	Dosage (mg)	Mean of mean arc sizes (deg)	Std. dev. of arc size within tracks (deg)	Mean of mean arc sizes (deg)	Std. dev. of arc size within tracks (deg)	Mean of mean arc sizes (deg)	Std. dev. of arc size within tracks (deg)
30	1	90.4	62.1	82.5	57.4	91.2	53.6
	10^{-1}	96.8	60.2	106.4	56.2	97.0	49.7
	10^{-2}	79.4	64.6	72.4	55.6	79.7	49.6
	10^{-3}	86.6	63.6	83.1	49.8	93.3	64.9
	10^{-4}	96.0	73.7	93.7	63.5	89.6	66.9
	control	62.8	55.1	60.5	40.1	80.8	53.7
Mean, not including control				87.6 ± 12.9	56.5 ± 4.9	90.1 ± 6.5	56.9 ± 8.4
60	1	96.9	66.8	101.7	61.2	91.0	54.8
	10^{-1}	86.5	58.7	93.4	57.2	80.2	52.5
	10^{-2}	74.4	66.6	80.7	65.3	64.8	48.0
	10^{-3}	85.0	65.8	98.2	52.0	78.3	56.4
	10^{-4}	98.7	60.4	91.5	67.5	92.6	49.2
	control	53.5	51.2	51.0	46.1	73.8	47.5
Mean, not including control				93.1 ± 8.0	60.6 ± 6.2	81.4 ± 11.2	52.2 ± 3.6

TABLE 2. REGRESSIONS OF ABSOLUTE TURN ANGLE AT EACH DATA POINT VS. ABSOLUTE HEADING

Dosage (mg)	Diffusion period (min)	Number of turns	Intercept (degs)	P^a	Slope (degs/deg)	P	Correlation coefficient (r)
1.0	30	1289	30.5	<0.0001	0.075	<0.0001	0.119
10^{-1}	30	1308	26.2	<0.0001	0.092	<0.0001	0.160
10^{-2}	30	790	27.6	<0.0001	0.044	0.033	0.067
10^{-3}	30	487	25.5	<0.0001	0.086	0.0005	0.151
10^{-4}	30	729	25.5	<0.0001	0.038	0.040	0.066
1.0	60	1136	29.0	<0.0001	0.116	<0.0001	0.173
10^{-1}	60	1462	26.9	<0.0001	0.076	<0.0001	0.132
10^{-2}	60	1162	22.8	<0.0001	0.044	0.002	0.087
10^{-3}	60	540	24.1	<0.0001	0.011	0.516	0.033
10^{-4}	60	526	25.0	<0.0001	0.039	0.078	0.063

[a] Probability of observing a T statistic larger than the observed T given that H_0 is true. H_0: value of parameter = 0.

The slopes of the regressions were often significant and always positive, although they were low (Table 2). Thus, the beetles tended to have slightly larger turn angles at higher headings.

In the analysis of the net (actual) heading of a beetle at a point as compared to the net turn angle that was subsequently made at that point, the regressions showed the slopes were highly significant (Table 3), but they were in the range of −0.1 to −0.2, and the correlation coefficients were in the range of −0.15 to −0.30. The sign of a turn angle therefore had a weak tendency to be opposite to the sign of the heading at that point.

Frequency histograms of the maximum absolute heading between occurrences of headings of 0° suggested that the distributions on the full circle were centered about 0° and fell off gradually towards the higher angles, with a small peak at 180+° (Figures 2 and 3). There was no consistent sign of any peak at intermediate angles, although there was a suggestion of peaks at 50–70° and 90–110°. Most of the maximum headings were less than 90°. However, headings between 90 and 180° were not uncommon. Calculations from the regressions of maximum heading versus distance to the source further showed that, on average, turns back towards the source were initiated at about 70°, even at the release point of the beetles (Table 4).

The heading decreased gradually as the source was neared, becoming steeper within 1–5 cm of the source (Figures 4 and 5). Turn radius decreased as the source was neared (Figure 6) (Akers, 1985).

TABLE 3. REGRESSIONS OF ACTUAL TURN ANGLE AT EACH DATA POINT VS. ACTUAL HEADING

Dosage (mg)	Diffusion period (min)	Number of turns	Intercept (degs)	P^a	Slope (degs/deg)	P	Correlation coefficient (r)
1.0	30	1289	−2.00	0.097	−0.159	<0.0001	−0.261
10^{-1}	30	1308	0.05	0.962	−0.116	<0.0001	−0.218
10^{-2}	30	790	−1.20	0.396	−0.115	<0.0001	−0.218
10^{-3}	30	487	−2.92	0.091	−0.104	<0.0001	−0.188
10^{-4}	30	729	−2.36	0.082	−0.072	<0.0001	−0.157
1.0	60	1136	0.10	0.939	−0.203	<0.0001	−0.308
10^{-1}	60	1462	1.05	0.328	−0.105	<0.0001	−0.198
10^{-2}	60	1162	3.16	0.001	−0.065	<0.0001	−0.149
10^{-3}	60	540	4.82	0.0003	−0.093	<0.0001	−0.223
10^{-4}	60	526	1.22	0.449	−0.078	<0.0001	−0.171

[a] Probability of observing a T statistic larger than the observed T given that H_0 is true. H_0: value of parameter = 0.

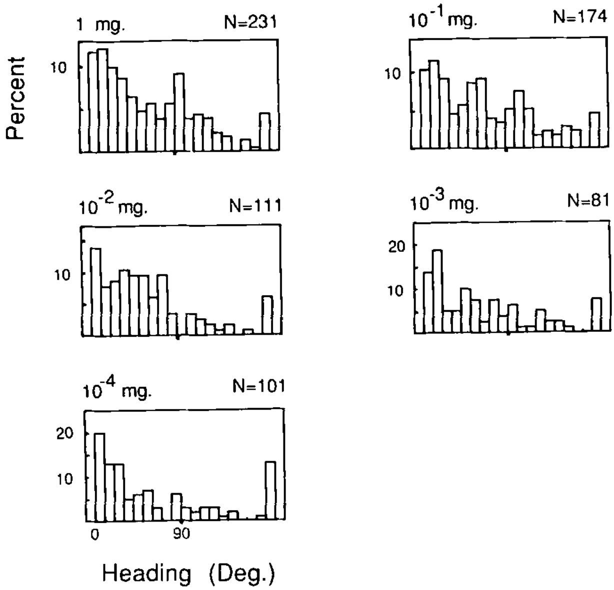


FIG. 2. The number of occurrences of maximum headings within each 10° interval after having turned from a heading of 0° and before returning to it. Data are from each treatment in the experiment with the 30-min diffusion period. N = total number of maximum headings in treatment.

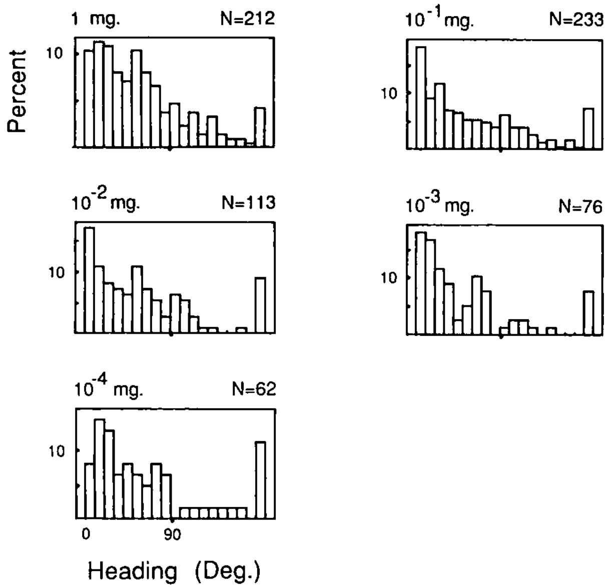


FIG. 3. The number of occurrences of maximum headings within each 10° interval after having turned from a heading of 0° and before returning to it. Data are from each treatment in the experiment with the 60-min diffusion period. N = total number of maximum headings in treatment.

TABLE 4. REGRESSIONS OF MAXIMUM HEADING ON EACH ARC VS. DISTANCE FROM SOURCE

Dosage (mg)	Diffusion period (min)	Number of arcs	Intercept (degs)	P[a]	Slope (degs/cm)	P	Correlation coefficient (r)
1.0	30	231	42.8	<0.0001	1.94	<0.0001	0.267
10^{-1}	30	174	32.8	<0.0001	2.98	<0.0001	0.447
10^{-2}	30	111	54.8	<0.0001	0.31	0.656	0.085
10^{-3}	30	81	37.7	0.002	2.30	0.024	0.226
10^{-4}	30	101	31.4	0.007	2.65	0.002	0.285
1.0	60	212	45.2	<0.0001	1.77	0.002	0.200
10^{-1}	60	233	32.2	<0.0001	2.66	<0.0001	0.364
10^{-2}	60	113	67.9	<0.0001	−0.67	0.392	0.048
10^{-3}	60	76	34.7	0.080	1.47	0.002	0.167
10^{-4}	60	62	44.4	0.002	2.07	0.061	0.204

[a] Probability of observing a T statistic larger than the observed T given that H_0 is true. H_0: value of parameter = 0.

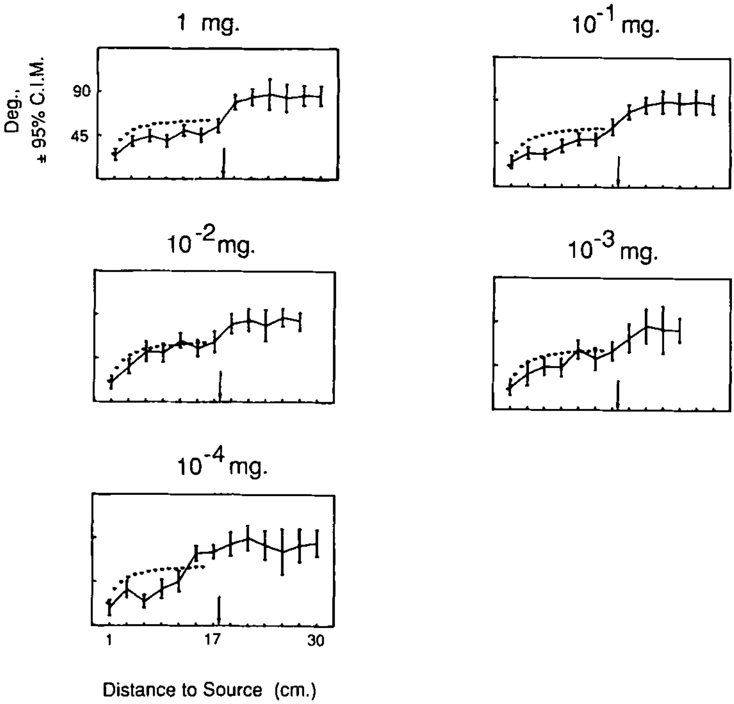


FIG. 4. The effect of distance from the source on the mean gross heading in the experiment with the 30-min diffusion period. Error bars show the 95% confidence interval of the mean. Dotted lines show headings predicted by a model based on counterturns initiated by a decrease in the rate of increase of concentration. Arrow marks the approximate release point of the beetles.

DISCUSSION

Since Fraenkel and Gunn (1961) published their benchmark work on orientation, the many mechanisms that are potentially available to an animal for orientation have gradually become more evident (e.g., Mittelstadt-Burger, 1972; Jander, 1975; Kennedy, 1977a,b, 1978, 1983, 1986; Bell and Tobin, 1982). The mechanisms the beetles used to orient to a point source in still air were inferred from a set of hypotheses about the characteristics of track form produced by each of several possible mechanisms. Measurements were found or devised to describe different characteristics of track form, and then the observed measurements were compared to those that were expected from each of the mechanisms. However, while analyses such as the present one may be strongly

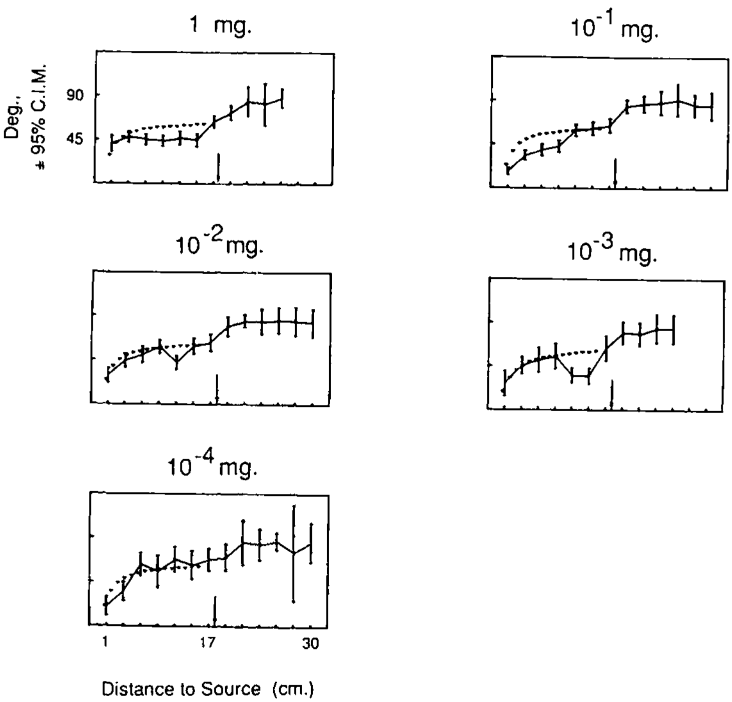


FIG. 5. The effect of distance from the source on the mean gross heading in the experiment with the 60-min diffusion period. Error bars show the 95% confidence interval of the mean. Dotted lines show headings predicted by a model based on counterturns initiated by a decrease in the rate of increase of concentration. Arrow marks the approximate release point of the beetles.

suggestive, they cannot be completely conclusive without further experiments that isolate individual mechanisms (Bell and Tobin, 1982; Kennedy, 1977b). Because of the considerable state of flux in the theory and terminology of orientation, each mechanism will be explicitly defined as it is considered. They will be discussed using the terminology of Fraenkel and Gunn (1961), as extended by Kennedy (1986) and herein. Although Kennedy developed many of his ideas while working with anemotactic situations, with some care they can be extended to a purely chemotactic situation, as will be attempted here.

The counterturning schemakinesis best explained the observed results if the cue used to initiate the counterturns was a decrease in the rate of increase of concentration. It was further necessary to postulate that the beetles have some innate tendency to compensate for the size of a previous arc in the opposite direction (Mittlestadt-Burger, 1972). In a schemakinesis, an animal uses infor-

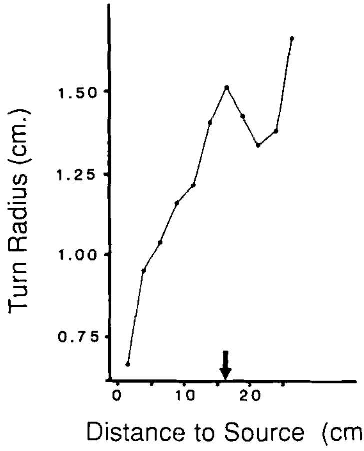


FIG. 6. An example of the relationship between distance from the source and the mean turn radius, as calculated from the walking and gross turning rates within 2.54-cm increments of radius from the source. Data are from the 1-mg dosage with a 60-min diffusion period. Arrow marks the approximate release point of the beetles.

mation concerning the behavior of stimulus intensity through time, combined with proprioceptive or central information concerning its own movements, to guide its path to the source (Kennedy, 1986). This is unlike many of the more classic mechanisms, where the animal is guided towards the source primarily by information on its position or orientation relative to the geometry of an intensity gradient (Fraenkel and Gunn, 1961). In the counterturning schemakinesis, an animal turns in one direction until it senses a critical sensory cue, at which time it initiates a turn in the opposite direction (Kennedy, 1986).

In a purely tactic situation, the environmental cue used to initiate a counterturn will strongly affect the form of the track. For example, consider an animal moving in a radial gradient, wherein contour lines of equal concentration form a series of concentric circles. If an animal depends upon a decrease in intensity to initiate a counterturn, each arc will have to obtain a heading beyond 90° before the animal can encounter such a decrease, because the animal does not move away from the source at headings less than 90°. On the other hand, an animal could use the rate of increase of intensity to initiate counterturns before a heading of 90°. As heading decreases towards 0°, the rate of increase of concentration increases, while as heading increases away from 0°, the rate decreases. The rate of increase of intensity begins to decrease when a heading of 0° is crossed.

Counterturning is consistent with the unimodal distribution of turn angle sizes (Figure 1). Turning is essentially constant in this mechanism, and there is nothing to cause two or more classes of turn angle size, such as might occur if straight sections were interspersed with tight arcs.

The beetles' movements were irregular and noisy, as indicated by the analysis of arc size (Table 1) (examples of trails are shown in Figure 7 of Akers and Wood, 1989a). Counterturning is consistent with such noise, because the counterturns are initiated largely or entirely by sensory input and therefore are liable to the full effects of sensory noise.

The comparison of absolute heading at a point with the absolute turn angle made at that point indicated that turning rate remained moderate even at headings near 0° (Table 2), meaning that the beetles had no tendency to fix on a heading directly towards the source. This is entirely consistent with counterturning. However, the beetles also tended to have slightly larger turn angles at higher headings. There is no clear reason why counterturning alone ought to produce larger turn angles at larger headings. However, there are two possible contributing factors. First, the beetles may have some innate tendency to initiate arcs in the direction opposite to the current arc, and this tendency may grow stronger the longer it takes to be released by sensory cues. There is some support for this suggestion. Beetles in control situations do not have gross turning rates low enough to account for their low net turning rates (Akers, 1985; Akers and Wood, 1989a). In other words, control beetles have much straighter paths overall than would be the case if all their turn angles were of one sign. Therefore, the beetles probably have some innate tendency to compensate for the size of a previous arc. Mittelstadt-Burger's work also supports the possibility of an innate counterturning tendency that compensates for the size of a previous arc (Burger, 1971; Mittelstadt-Burger, 1972), and Kramer (1975) found that moths walking in pheromone-free wind periodically reverse their heading with respect to the wind in a manner that produces fairly direct movement overall. The second possible mechanism that could produce larger turn angles at higher headings is a change in the cue used to initiate a counterturn as heading changed, from a decrease in the rate of increase of concentration to a decrease in concentration itself. However, while exploratory graphs showed turn angle increasing as heading increased, no pattern was consistent enough to allow a decision on this second possibility.

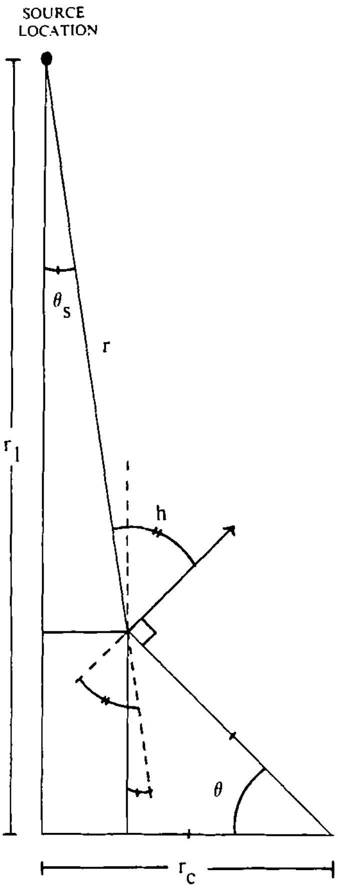
Compensated counterturning is consistent with the low slope and correlation coefficient observed in the comparison of the net (actual) heading of a beetle at a point with the net turn angle that was subsequently made at that point (Table 3). In counterturning, turn angles would be away from as well as towards a heading of 0°, which would decrease the correlation, but if there were compensation for the size of a previous arc, the slope would be negative.

The analysis of the maximum absolute heading between occurrences of headings of 0° (Figures 2 and 3) gave the first indication that, if counterturning were in operation, a cue for counterturn initiation was likely to be a decrease in the rate of increase of concentration. Most maximum headings occurred before 90°, the heading beyond which a decrease in concentration becomes possible. These counterturns, then, could not have been initiated by a decrease in concentration. Calculations from the regressions of maximum heading versus distance to the source further showed that, even at the release point of the beetles, counterturns were initiated at about 70°, on average (Table 4), consistent with the possible minor peak in maximum headings at 50–70°. In addition, counterturning could produce a distribution centered near 0°, if the cue used to initiate counterturns were a decrease in the rate of increase of concentration, because the rate of increase begins to decrease just as a heading of 0° is crossed. Finally, counterturning has no difficulty explaining those maximum headings that occurred between 90 and 180°, because these counterturns could have easily been initiated by a decrease in concentration. A decrease in concentration would begin to occur just beyond 90°, where the second possible minor peak in maximum heading also appears to lie.

Counterturning was also best able to explain the form of the decrease in heading as the source was neared (Figures 4 and 5), but only if the cue used to initiate counterturns was a decrease in the rate of increase of concentration. If a counterturn were initiated by a decrease in concentration, heading would not decrease much, because, at any distance, the animal still must head away from the source, i.e., at a heading of greater than 90°, to encounter a decrease in concentration. If the animal used a decrease in the rate of increase to trigger a counterturn, we need to know how concentration changes with heading as the animal turns, in order to predict how heading would decrease as the source is neared. If we assume that the beetles move along roughly circular arcs, then the rate of change of distance to the source with respect to heading can be determined (Figure 7). The relationship between concentration and distance to the source may then be substituted into the equations. This latter relationship was estimated from gas–liquid chromatography data, under the assumption that the gradient is circular (Akers and Wood, 1989a).

In order to better visualize the behavior of the system, the equations were evaluated at 1° intervals over arcs of 0° to 90°, using a computer to carry out the calculations. If turn radius is held constant, the rate of increase decreases more rapidly with heading the closer an arc is to the source, but decreasing turn radius can strongly offset this effect (Akers, 1985). The effect of changing turn radius can be taken into account by calculating the turn radius from regressions relating the walking and turning rates to distance from the source (see Methods and Materials). For the purposes of exploration (Figure 8), the regression parameters used to estimate the turn radii were the means over all treatments except the control.

The rate of increase is always maximal at a heading of 0°, directly towards the source, and falls to 0 at 90°, where the animal is moving neither away from



$$r^2=(r_1-r_c\sin\theta)^2+(r_c-r_c\cos\theta)^2$$

$$r=(r_1^2-2r_cr_1\sin\theta-2r_c^2+2r_c^2)^{\frac{1}{2}}$$

$$\frac{dr}{d\theta}=\frac{r_c^2\sin\theta-r_cr_1\cos\theta}{r}$$

$$\begin{aligned}h&=(90-(90-\theta))+\theta_s\\&=\theta+\theta_s\\&=\theta+\arctan\left[\frac{r_c-r_c\cos\theta}{r_1-r_c\sin\theta}\right]\end{aligned}$$

$$\frac{dh}{d\theta}=\frac{r_1^2-r_cr_1\sin\theta-r_c^2\cos\theta+r_c^2}{r^2}$$

Where:

r =distance from beetle to source
r_1 =distance at which arc was initiated (heading=zero degs.)
r_c= turn radius of arc
h =heading angle of beetle
θ =angle turned by beetle along arc

The relationship between heading and motion along the arc is a one-to-one mapping, at least when $r_c<r_1$ and h<90 deg. Therefore the derivative of the function relating arc angle to heading is the inverse of the derivative of the function relating heading to arc angle. that is,

$$\frac{d\theta}{dh}=\frac{1}{\frac{dh}{d\theta}}.$$

Then, by the chain rule,

$$\frac{dr}{dh}=\frac{dr}{d\theta}\frac{d\theta}{dh}=\frac{dr}{d\theta}\frac{1}{\frac{dh}{d\theta}}$$

FIG. 7. The geometry and equations needed to analyze the rate of change of distance from the source with respect to heading. The animal is assumed to turn along circular arcs of turn radius r_c.

or towards the source (Figure 8). Any arbitrarily chosen amount of decrease from the maximum is still reached at considerably lower headings as the source is neared, despite the accounting for the decrease in turn radius. For example, if the animal were sensitive to an absolute decrease of 0.01 units, heading would be expected to decrease in a strongly linear manner as the source was neared (Figure 9). The linear relationship and especially the steepness of the decrease

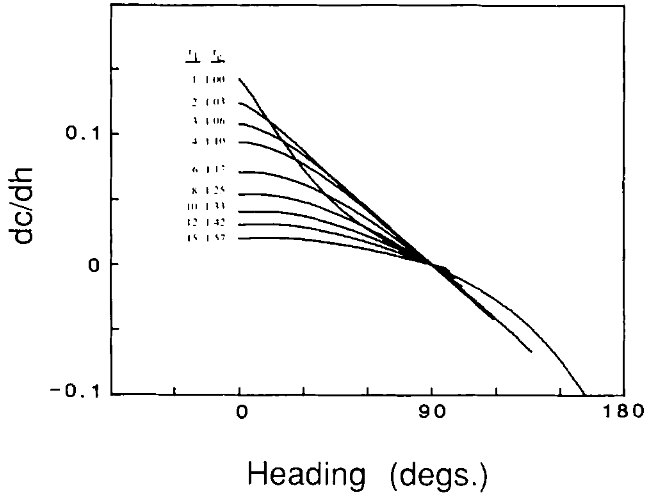


FIG. 8. An example of the effects of heading, turn radius, and distance of arc initiation from the source of pheromone on the rate of change of concentration with respect to heading, under the assumptions of a radial gradient and circular arcs. The y axis units are arbitrary and derive from a gradient decreasing exponentially with distance from the source and with concentration at the source arbitrarily set to one. r_i and r_c are defined in Figure 7. The r_c for each r_i was calculated from regressions relating the walking and gross turning rates to distance from the source. The parameters used in the regression equations were the means of the parameters over all treatments but the control.

is different from that seen in the data (Figures 4 and 5). On the other hand, if the animal were, for example, sensitive to a 50% decrease from the maximum rate of increase, heading would decrease gradually farther from the source, becoming steeper as the source was neared (Figure 9).

If the animal indeed initiated a counterturn when it just perceived a change in the stimulus, counterturn initiation would occur at the "just noticeable difference" of psychophysics, and the behavior of the headings might be expected to follow the classic Weber's and Fechner's laws. These laws state that the difference in stimulus intensity needed to obtain a just noticeable difference in sensation magnitude is proportional to the original stimulus intensity (Gescheider, 1976). Therefore, a model based on a proportionate decrease is also physiologically reasonable.

The dotted lines in Figures 4 and 5 show the predicted changes in heading as the source is neared, for a counterturning schemakinesis when the cue is a 50% decrease in the rate of increase. The turn radii were calculated using the respective parameters for the regressions of walking and turning rate in each

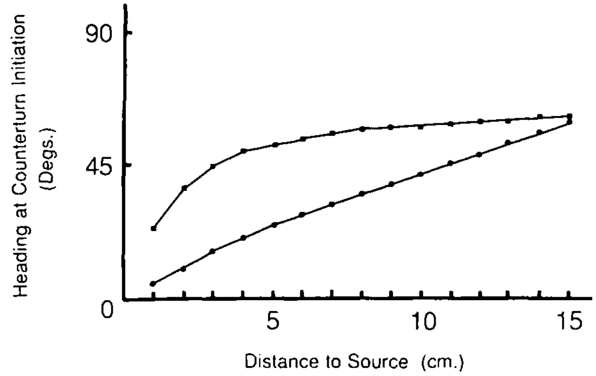


FIG. 9. The predicted headings at counterturn initiation derived from Figure 8 and under the assumption that counterturns are initiated by either an absolute decrease of 0.01 units from the maximal rate of increase (lower curve, circles) or a proportional decrease of 50% from the maximal rate of increase of concentration (upper curve, squares). Each point on a curve is derived by finding the curve in Figure 8 that has the same distance from the source as that point, then moving down from the maximum rate of increase on that curve until the chosen critical decrease from the maximum is reached. The heading at which that decrease was reached is then read from the horizontal axis.

treatment. While somewhat arbitrary, a 50% decrease was chosen because it produced critical headings of about 60° at the starting distance of 15 cm from the source. Values of 45–65° are typical for the mean gross headings at that distance. Although the analysis required several simplifying assumptions, the predicted curves often approximate the actual data in form, if not actually lying on the line (Figures 4 and 5). This is particularly true in the 60-min experiment (Figure 5). Perhaps a slight difference in the shape of the gradient in the 30-min experiment was responsible for the slightly steeper decreases in heading observed in that experiment (Figure 4). The relationship between concentration and distance from the source was estimated using data from the 60-min diffusion period (Akers and Wood, 1989a), while no information is available on the exact form of the gradient in the 30-min experiment.

A similar process of comparing expected and observed results was applied to each of the other possible mechanisms of orientation. Each appeared to be inconsistent with at least some observations. The classic tropotaxis is inconsistent with several of the results. In the tropotaxis, symmetrically placed receptor organs permit simultaneous comparisons of intensity in space. If the organism turns towards the receptor with the greater intensity, it will turn towards the source. If it can then balance the stimuli efficiently on its receptors, its path to the source should be very direct (Fraenkel and Gunn, 1961).

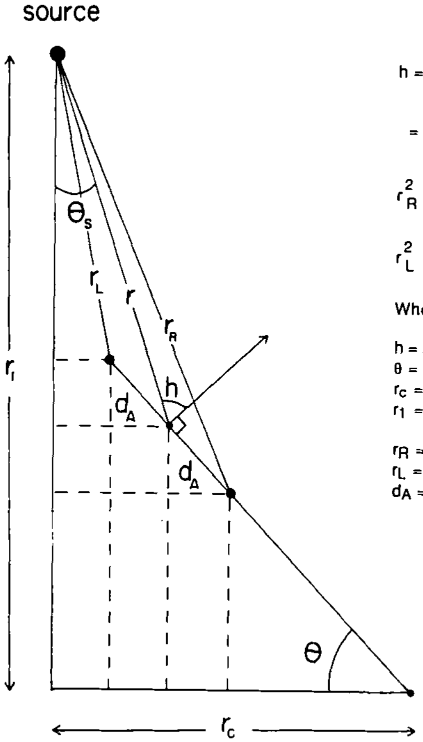
The paths of the beetles towards the source were generally far from direct (Figure 7 in Akers and Wood, 1989a), and the beetles were turning almost continuously. The comparison of the gross (absolute) heading of a beetle at a point with the gross turn angle that was subsequently made at that point (Table 2) showed that the beetles continued to have moderate rates of turning even when they were headed almost directly towards the source. Thus, the beetles never appeared to fix on a heading near 0°. In addition, in the regressions of the net (actual) heading of a beetle at a point on the net turn angle that was subsequently made at that point (Table 3), the slopes were in the range of −0.1 to −0.2, and the correlation coefficients were in the range of −0.15 to −0.30. If the animal was perfectly tropotactic, and given the conventions by which the signs of angles were defined, the regressions should have had a slope of −1.0 and a correlation coefficient of −1.0 (Bell and Tobin, 1981). These observations, then, are inconsistent with an efficient tropotaxis. However, an inefficient tropotaxis, where the animal cannot accurately balance the intensity on the two receptors, is still a possibility. Such a tropotaxis is consistent with the above results, with a unimodal distribution of turn angle sizes (Figure 1), and with the increase in turn angle size as heading increased away from 0° (Tables 2 and 3).

Nevertheless, a tropotaxis cannot explain those maximum headings of 90° to 180° that occurred between occurrences of headings of 0° (Figures 2 and 3). The difference between the antennae in distance to the source reaches a maximum at a heading of 90° and then begins to decrease again as the animal turns away from the source. If a tropotactic animal does not perceive the difference in concentration by the time it achieves a heading of 90°, that difference will once again begin to decrease and make it even less likely that the animal will initiate a return towards the source. It would more likely continue on until it completes a circle. The possible minor peak in maximum heading, which appears to occur at about 90–110°, could be attributed to tropotaxis, but the argument would seem more satisfactory if the peak were centered just before 90° rather than beyond it.

Neither is the tropotaxis consistent with the form of the decrease in heading as the source was neared or with the decrease in turn radius. As distance from the source decreases, smaller separations in space should be needed to obtain the same amount of information concerning the gradient. In a tropotaxis, the difference in intensity between two receptors separated by some fixed distance will increase, thereby improving its possible efficiency. Accordingly, heading should decrease. However, since the animal should then head more linearly to the source as the source is neared (Fraenkel and Gunn, 1961), turn radius should increase. This is opposite to the behavior observed (Figure 6) (Akers, 1985).

Furthermore, although an inefficient tropotaxis might be expected to cause a decrease in heading as the source was neared, the expected form of the decrease does not fit the data. An analysis similar to that done for the counterturn was done for the tropotaxis (Figure 10) and predictions made as to the heading at which the animal would encounter a concentration difference large enough between its antennae to cause it to turn back towards the source after having once turned away (Figure 11). Again, for Figure 11, the critical concentration difference was taken to be that which occurred at a heading of 60° and a distance of turn initiation of 15 cm, and the parameters of the regressions for the walking and turning rates were the means of the parameters of all treatments but the control. The receptors were treated as point receptors in this analysis, but this is a reasonable estimate given the beetle's club-shaped antenna.

Two points become apparent from this analysis. First, neither curve fits the observed data (Figures 4 and 5). Second, the difference in concentrations between antennae at a distance of 15 cm and a heading of 60° is on the order of 3%. The animal must be able to detect this difference if the tropotaxis is to



$$h = \theta + \theta_s$$

$$= \theta + \arctan\left[\frac{r_c - r_c\cos\theta}{r_1 - r_c\sin\theta}\right]$$

$$r_R^2 = [r_1 - (r_c - d_A)\sin\theta]^2 + [r_c - (r_c - d_A)\cos\theta]^2$$

$$r_L^2 = [r_1 - (r_c + d_A)\sin\theta]^2 + [r_c - (r_c + d_A)\cos\theta]^2$$

Where:

h = heading angle
θ = angle of arc along the turn the beetle is making
r_c = turn radius of arc along which the beetle is turning
r_1 = distance from the source at which a turn is initiated, ie., when h = zero deg.
r_R = distance from source to right antenna
r_L = distance from source to left antenna
d_A = distance between midline and antenna

FIG. 10. The geometry and equations needed to analyze the difference in distance to the source between two point receptors placed symmetrically about an animal's midline. The animal is assumed to turn along circular arcs.

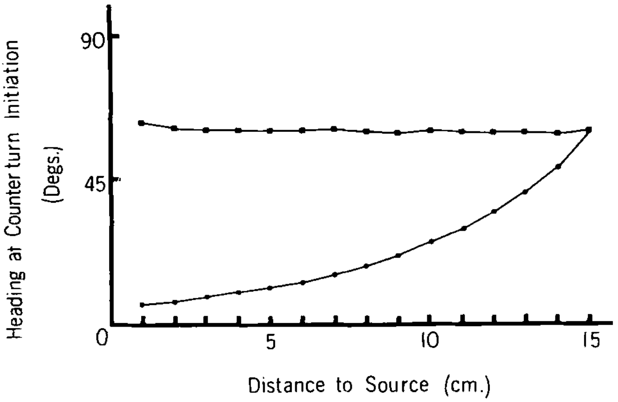


FIG. 11. The headings at which an animal would turn back towards the source after having once turned away, as predicted by an inefficient tropotaxis which requires either a critical absolute (lower curve, circles) or proportional (upper curve, squares) difference in concentration between the antennae before a return towards 0° can occur.

function. However, this implies a Weber fraction of 0.03, considerably lower than the values of 0.3–1.5 that have been obtained for other animals and modalities (Gescheider 1976). The few direct measurements that have been made on insects indicate that the ability to detect a 3% difference may be an order of magnitude better than any performance previously observed (Martin, 1964; Kramer, 1975; Bell and Tobin, 1982). On the other hand, the 50% decrease for counterturn initiation is within the usual range for Weber fractions.

Both the classic klinotaxis of Fraenkel and Gunn (1961) and a closely related modification of it are also inconsistent with several of the behavioral observations. In the classic klinotaxis, short "wigwags" of the receptor organs are made to either side of the body and information on the stimulus intensity in space is obtained by comparing stimulus intensity through time. The wigwags are herein assumed to be generated within the central nervous system. Oriented maneuvers are made on the basis of information obtained about the symmetry of the gradient during the wigwags. However, unless the wigwags are large enough that the concentrations can be made different enough at the ends of the swings, a classic klinotactic movement will not gain the animal much information regarding the form of the gradient (Kennedy, 1986).

A small modification to the classic klinotaxis overcomes this problem. Since it would generate a pattern that appears analogous to the zigzagging behavior of flying moths (Kennedy, 1983), it shall be referred to as the zigzagging mechanism. The animal still obtains information concerning the symmetry of the gradient as it executes centrally generated arcs, but the two mechanisms differ in scale. In the classic klinotaxis, the arcs are executed by swinging the anterior portion of the body back and forth, and the size of each wigwag is smaller than the body length of the animal, or certainly very little more. In the modified klinotaxis, the arcs may be many body lengths of the animal and are executed by a regular alteration of the walking pattern. Straight sections between arcs could also occur.

The small wigwag movements that would be expected under a klinotaxis are inconsistent with the size of movements made by the beetles. The beetles are 4-6.5 mm long, and their turn radii were typically in the range 0.7–1.5 cm (Figure 6). The circumferences of the arcs made by the beetles therefore averaged two to five body lengths, clearly much larger than would be expected of the klinotaxis. However, such arcs would easily be consistent with zigzagging. Zigzagging is also consistent with the unimodal distribution of turn angle sizes, if no straight sections occurred between arcs (Figure 1). In addition, zigzagging is consistent with a moderate rate of turning even at headings close to 0°, although there is no clear reason why zigzagging should produce larger turn angles as heading increased, or why these turn angles should compensate in sign for the heading (Tables 2 and 3).

Further, zigzagging is inconsistent with the noise apparent in the movements of the beetles (Figure 7 in Akers and Wood, 1989a). This was also indicated by the analysis of the variation of arc sizes (Table 1), which failed to demonstrate the low level of variation that might be expected from regular, oscillatory movements. The turns in zigzagging are herein postulated to be driven largely by a central pattern generator, and such movements tend to be regular, especially once they have come into balance with environmental requirements (review in Camhi, 1984). Examples of such movements may be found in leg movements in walking, wing movements in flight, swimmeret movements, leech swimming movements, and respiratory movements. Even the zigzagging of moths in a windstream may be driven by a central pattern generator (Kennedy, 1983, 1986), although there is now some renewed controversy on this point (Preiss and Kramer, 1986). Coefficients of variation for moths zigzagging in an odor plume appear to be 20–30% (Kuenen and Baker, 1983; Cardé et al., 1984). By contrast, the beetles' movements are highly irregular, with coefficients of variation in the range of 60–90% (calculated from Table 1). Since variation was always fairly high, rigid zigzagging seems unlikely.

Zigzagging was also inconsistent with the distribution of maximum headings between occurrences of 0°, which was centered about a heading very close to 0° (Figures 2 and 3). Zigzagging might have been expected to produce maximum headings centered some distance from 0°, as the animal turned on its regular, centrally defined arcs. For instance, track headings of the straight sections in zigzagging moth flight are generally in the range of 30–90° with respect to the wind (Kuenen and Baker, 1983; Cardé et al., 1984; Kennedy et al., 1980; Farkas et al., 1974).

Zigzagging was also inconsistent with the notable decrease in heading as the source was neared (Figures 4 and 5). Since the turns in zigzagging are postulated to be under central control, heading should not change much under this mechanism, despite possible changes in sensory stimulation. However, the path might become narrower as the source was neared, which would be reflected in a decrease in turn radius (Akers, 1985).

Two other possible orientation mechanisms became apparent during the course of this analysis, but they also appeared to be inconsistent with the results. The first is a modification of the zigzagging mechanism and was termed the "look and leap." In zigzagging, oriented movements have to interact with instructions for movements arising from the basic turn-pattern generator, or else the animal would probably never reach a source. In the look and leap, the animal separates movements to gather information from oriented movements, in order to minimize the amount of turning. It first initiates an orientation movement, based on an endogenously generated pattern of turns, during which it obtains information about the symmetry or form of the gradient. Based upon this sensory information and information concerning the form of its own movements, the animal estimates the direction towards the source, and aligns itself with it. It then continues in a more or less linear fashion until an endogenous or sensory cue triggers another orientation maneuver. Apparently, some flies use a similar mechanism to orient with respect to the wind in response to an odor cue (the "aim first, then shoot" mechanism, Bursell, 1984; Hawkes and Coaker, 1979; Miller and Strickler, 1984; Kennedy, 1986).

The second mechanism is termed the "steepest-ascent schemakinesis." If an organism could efficiently measure the rate of change of the stimulus, it might attempt to identify that heading with the steepest rate of increase in intensity, which would be directly towards the source. The path might be expected to consist of relatively straight segments, during which the animal would determine the rate of increase along that heading, punctuated by sharp turns.

In both the above mechanisms, linear sections of track are interspersed with bouts of rapid turning. They might then be expected to generate a bimodal distribution of turn angle sizes (Figure 1), which was not observed. However, the sharp turns in the steepest ascent might be relatively rare, and thus perhaps obscured in a distribution. Furthermore, both mechanisms could conceivably operate without the appearance of a bimodal distribution of turn angles or turn radii. If an animal had relatively regular turn angles at every point on its track, it could create relatively linear sections by alternating the signs of the turn angles and larger arcs by holding the sign constant for a period of time. I have not yet conceived a simple measurement that would reflect such a behavior. Such behavior is not obvious in samples of tracks (Figure 7 in Akers and Wood, 1989a) and it seems difficult to reconcile with the variation in turn angle size (Figure 1). Nonetheless, the possibility cannot be completely excluded. Otherwise, the steepest ascent schemakinesis is inconsistent with the nearly constant turning executed by the beetles, and the beetles never seemed to head very directly towards the source, which also might have been expected. In the look-and-leap mechanism, the animal is also postulated to fix on a heading towards the source, once it estimates its direction from the orientation maneuver. Accordingly, it should not turn much for a period while on a heading near 0°, while at higher headings its turn angles should generally be considerably larger. However, the comparison of the absolute headings and turn angles at a point on the track showed that the beetles continued to have moderate rates of turning even when they were headed almost directly towards the source (Table 2). Combined with the lack of any regular movements and the unimodal turn angle size distribution, the beetles apparently did not look and leap very well.

In summary, the numerical analysis of the behavioral responses indicated that a compensated counterturning schemakinesis was most consistent with the observations, if the sensory cue used to initiate a counterturn was a decrease in the rate of increase of concentration. However, this raises the question of whether a beetle could detect such a cue at all. Concentration itself increases only about 30% as the animal swings from a heading of −90° to 90°, or vice versa. The detection of this increase itself would imply a Weber fraction of 0.3, relatively low by classic psychophysics. Detection of a rate of increase would require comparing at least two successive increases within this interval. On the other hand, Kramer (1978) has indicated that moths can detect a decrease of as little as 1%/sec, if continued for 5 sec. If this is true of the beetles as well, then they could possibly make the comparisons necessary for the mechanism to function. Finally, the possible effects of habituation have not been addressed in this paper. Because the animal is moving in a gradient, the stimulus is constantly changing, and thus any habituation is very difficult to isolate in the present experiment. However, in a preliminary experiment on the purely kinetic effects of pheromone (Akers, 1985), pheromone was applied as uniformly as possible to the arena, in an attempt to minimize any gradients. In that experiment, walking and turning rates were very similar between early (0–10 sec) and late (45–55 sec) portions of the track, giving at least some indication that pheromone perception habituates only slowly in this species, if at all.

Acknowledgments—I thank J.K. Grace, M.W. Akers, R.W. Mankin, and D.L. Wood for helpful critiques of the manuscript. I am also grateful for the support and encouragement given by D.L. Wood. Studies supported in part by Agricultural Experiment Station Project No. 1778, "Classification, Bionomics, Ecology, and Control of Bark Beetles Infesting California Trees," and grants from the Chancellor's Patent Fund and Phi Beta Kappa Society.

REFERENCES

AKERS, R.P. 1985. Olfactory discrimination and orientation by female *Ips paraconfusus* Lanier (Coleoptera: Scolytidae) to components of the male pheromone. PhD thesis. University of California, Berkeley. 231 pp.

AKERS, R.P., and WOOD, D.L. 1989a. Olfactory orientation responses by walking female *Ips paraconfusus* bark beetles: I. Chemotaxis assay. *J. Chem. Ecol.* 15(1):3–24.

AKERS, R.P., and WOOD, D.L. 1989b. A response surface analysis of chemotaxis by female *Ips paraconfusus* to components of the aggregation pheromone. In preparation.

BELL, W.J., and TOBIN, T.R. 1981. Orientation to sex pheromone in the American cockroach: Analysis of chemo-orientation mechanisms. *J. Insect Physiol.* 27:501–508.

BELL, W.J., and TOBIN, T.R. 1982. Chemo-orientation. *Biol. Rev.* 57:219–260.

BURGER, M.L. 1971. Zum Mechanismus der Gegenwendung nach mechanisch auf gezwungener Richtungsanderung bei *Schizophyllum subulosum* (Julidae, Diplopoda) *Z. vergl. Physiol.* 71:219–254.

BURSELL, E. 1984. Observations on the orientation of tsetse flies (*Glossinia pallidipes*) to wind-borne odours. *Physiol. Entomol.* 9:133–137.

CAMHI, J.M. 1984. Neuroethology: Nerve Cells and the Natural Behavior of Animals. Sinauer Assoc., Sunderland, Massachusetts. 416 pp.

CARDÉ, R.T., DINDONIS, L.L., AGAR, B., and FOSS, J. 1984. Apparency of pulsed and continuous pheromone to male gypsy moths. *J. Chem. Ecol.* 10:335–348.

FARKAS, S.R., SHOREY, H.H., and GASTON, L.K. 1974. Sex pheromones of Lepidoptera. Influence of pheromone concentration and visual cues on aerial odor-trail following by males of *Pectinophora gossypiella*. *Ann. Entomol. Soc. Am.* 67:633–638.

FRAENKEL, G.S., and GUNN, D.L. 1961. The Orientation of Animals: Kineses, Taxes, and Compass Reactions. Dover Publications, New York. 376 pp.

GESCHEIDER, G.A. 1976. Psychophysics, Method and Theory. John Wiley & Sons, New York. 177 pp.

HAWKES, C., and COAKER, T.H. 1979. Factors affecting the behavioural responses of the adult cabbage root fly, *Delia brassicae*, to host plant odour. *Entomol. Exp. Appl.* 25:45–58.

JANDER, R. 1975. Ecological aspects of spatial orientation. *Annu. Rev. System. Ecol.* 6:171–188.

KENNEDY, J.S. 1977a. Olfactory responses to distant plants and other odor sources, pp. 67–92, *in* H.H. Shorey and J.J. McKelvey, Jr. (eds.). Chemical Control of Insect Behavior. John Wiley & Sons, New York.

KENNEDY, J.S. 1977b. Behaviorally discriminating assays of attractants and repellents, pp. 215–229, *in* H.H. Shorey and J.J. McKelvey, Jr. (eds.). Chemical Control of Insect Behavior. John Wiley & Sons, New York.

KENNEDY, J.S. 1978. The concepts of olfactory "arrestment" and "attraction." *Physiol. Entomol.* 3:91–98.

KENNEDY, J.S. 1983. Zigzagging and casting as a programmed response to wind-borne odour: A review. *Physiol. Entomol.* 8:109–120.

KENNEDY, J.S. 1986. Some current issues in orientation to odour sources, pp. 11–26, *in* T.L. Payne, M.C. Birch, and C.E.J. Kennedy (eds.). Mechanisms in Insect Olfaction. Oxford University Press, New York.

KENNEDY, J.S., LUDLOW, A.R., and SANDERS, C.J. 1980. Guidance system used in moth sex attraction. *Nature* 288:475–477.

KRAMER, E. 1975. Orientation of the male silkmoth to the sex attractant bombykol. pp. 329–335, *in* D.A. Denton and J.P. Coghlan (eds.). Olfaction and Taste, Vol. V. Academic Press, New York.

KRAMER, E. 1978. Insect pheromones, pp. 205-209, *in* G.L. Hazelbauer (ed.). Taxis and Behaviour. Chapman and Hall, London.

KUENEN, L.P.S., and BAKER, T.C. 1983. A non-anemotactic mechanism used in pheromone source location by flying moths. *Physiol. Entomol.* 8:277-289.

MARTIN, H. 1964. Zur Nahorientierung der Biene im Duftfeld zugleich ein Nachweis fur die Osmotropotaxis bei Insekten. *Z. Vergl. Physiol.* 48:481-533.

MILLER, J.R., and STRICKLER, K.L. 1984. Finding and accepting host plants, pp. 127-157, *in* W.J. Bell and R.T. Cardé (eds.). Chemical Ecology of Insects. Chapman and Hall, New York.

MITTELSTADT-BURGER, M.L. 1972. Idiothetic course control and visual orientation, pp. 275-279, *in* R. Wehner (ed.). Information Processing in the Visual System of Arthropods. Springer-Verlag, New York.

PREISS, R., and KRAMER, E. 1986. Mechanism of pheromone orientation in flying moths. *Naturwissenschaften* 73:555-557.

SILVERSTEIN, R.M., RODIN, J.O., and WOOD, D.L. 1966. Sex attractants in frass produced by male *Ips confusus* in ponderosa pine. *Science* 154:509-510.

WOOD, D.L., STARK, R.W., SILVERSTEIN, R.M., and RODIN, J.O. 1967. Unique synergistic effects produced by the principal sex attractant compounds of *Ips confusus* (LeConte) (Coleoptera: Scolytidae). *Nature* 215:206.