14 Able, K. P., J. exp. Biol. *141* (1989) 241.
15 Shurcliff, W. A., Polarized Light: Production and Use. Harvard Univ. Press, Cambridge, Mass., 1962.
16 Helbig, A. J., Dissertation. Frankfurt/M., 1989.
17 Viehmann, W., Behaviour *68* (1979) 24.
18 Batschelet, E., Circular Statistics in Biology. Academic Press, London 1981.
19 Zink, G., Der Zug europäischer Singvögel, vol. 1. Möggingen, 1973.
20 Wiltschko, R., and Wiltschko, W., Behav. Ecol. Sociobiol. *9* (1981) 135.
21 Bingman, V. P., Monit. zool. ital. (N. S.) *17* (1983) 395.
22 Able, K. P., and Bingman, V. P., Proc. 19th Int. Orn. Congr. 1988, p. 1932.
23 Wiltschko, W., and Wiltschko, R., Current Orn. *5* (1988) 67.
24 Waterman, T. H., and Forward, R. B. Jr, Exp. Zool. *180* (1972) 33.
25 Alder, K., and Taylor, D. H., J. comp. Physiol. *87* (1973) 203.
26 Taylor, D. H., and Adler, K., Science *181* (1973) 285.
27 Adler, K., and Phillips, J. B., J. comp. Physiol. *156A* (1985) 547.
28 Haidinger, W., Annln Phys. Chem. *63* (1844) 29.
29 Frisch, K. von, Experientia *5* (1949) 142.
30 Rossel, S., and Wehner, R., Nature *323* (1986) 128.

0014-4754/90/070755-04$1.50 + 0.20/0

Interpreting animal wall-following behavior

R. P. Creed Jr[a] and J. R. Miller

[a] W. K. Kellogg Biological Station, and the Department of Zoology, Michigan State University, 3700 East Gull Lake Drive, Hickory Corners (Michigan 49060, USA), and Department of Entomology, and the Pesticide Research Center, Michigan State University, East Lansing (Michigan 48824, USA)
Received 24 July 1989; accepted 8 December 1989

Summary. Using computer simulations and behavioral experiments with the American cockroach, we found that active vs passive (barrier-directed) wall-following can be readily distinguished and quantified by incorporating a range of convex curves into test arenas. Although previously considered strongly thigmotactic, more than 50% of running American cockroaches depart convex curves with diameters less than 1 m. A new framework for evaluating wall-following behaviors is presented.
Key words. Thigmotaxis; wall-following; cockroaches; orientation.

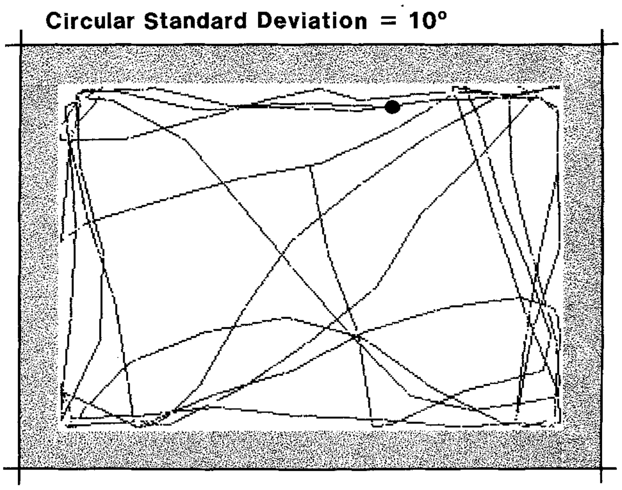
Wall-following is commonly taken as diagnostic of 'thigmotaxis', which is currently defined[1, 2] as the orientation of an animal in space by touch. The wall-following paths produced by thigmotactic animals are thought to be generated by minimizing departures from a surface once contact is established and a propensity to turn back quickly if contact is lost[3-5]. However, using Weston's[6] computer simulations of animal movement, we can generate a pattern of wall-following very similar to that of a thigmotactic animal simply by restricting the circular standard deviation of permissible turn angles for an otherwise random mover in a bounded arena (fig. 1 A–C). These movement simulations convincingly demonstrated that the apparent wall-following paths of straight running movers in an arena bounded by straight or concave walls (fig. 1 B, C) could easily be confused with true thigmotaxis. We suspect that this confusion abounds in the behavioral literature, including work of our own[7].

In light of the simulation results, we reasoned that incorporating convex curves into the walls of an arena (e.g. the hourglass arena, fig. 2 A) should help differentiate active from passive wall-following. A highly thigmotactic animal (active wall-follower) would be expected to hug the wall when following both convex and concave curves (fig. 2 A, path 1), while a pseudothigmotactic animal (passive wall-follower) would be expected to depart from the convex curves (fig. 2 A, paths 2 and 3). Furthermore, the strength of an animal's thigmotactic response could be quantified by scoring the percent of runs along convex curves of varying radii that result in departures.

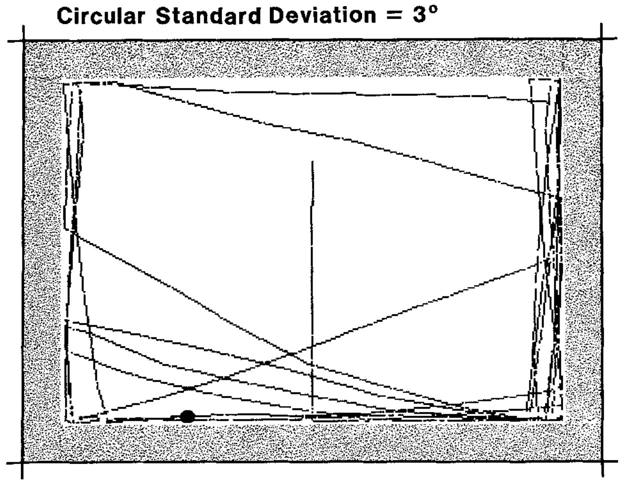
We tested these predictions using a laboratory strain of the American cockroach (*Periplaneta americana* L.), an animal considered strongly thigmotactic[8], but previously studied only in circular arenas. In our own preliminary studies of cockroaches using a 1 m diameter circular arena, walking *P. americana* (n = 10) spent 74% of their time in contact with the arena wall, and when running rarely departed (i.e. moved more than 1 antennal length) from the wall. While these data are consistent with Bell's[8] observations that *P. americana* is strongly thigmotactic, they do not exclude passive wall-following. We report here: 1) the results of two experiments which demonstrate that moving American cockroaches are not strongly thigmotactic and 2) a new conceptual framework for evaluating the wall-following behavior of animals.

Materials and methods

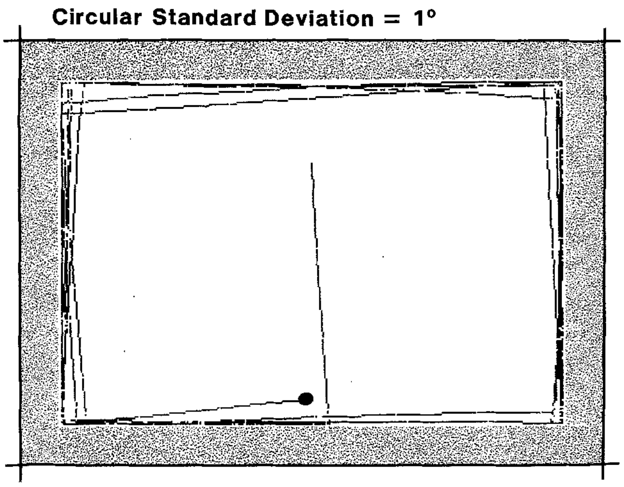
Hourglass arena experiment. The arena (fig. 2 A) was constructed by cutting a hole of desired shape in a 65 × 120 cm sheet of 2 cm thick plywood. A 15 cm high wall of flexible, Mylar™ plastic was glued to the sides of the cut-out. This movable arena was set on a sheet of heavy brown wrapping paper (changed for each experi-



A



B



C

Figure 1. *A–C* Increases in apparent wall-following as the paths of a computer simulated mover in a bounded arena become straighter due to increasingly restricted circular standard deviations. These tracks were printed from the monitor screen of an IBM XT microcomputer executing the 'restricted random' mover simulation of Weston[6]. The stepwise mover is initiated with a downward heading from the top center of the screen. After a step representing ca 1/20th the screen width, a new heading is selected at random from a distribution of possible new headings normally distributed (see respective assigned circular standard deviations [CSD], fig. 1) and centered around the heading of the previous step. Upon contacting the 'arena wall', the simulated mover expands the assigned CSD incrementally until a new, unimpeded heading is found whereupon another step commences and the original CSD is immediately re-employed.

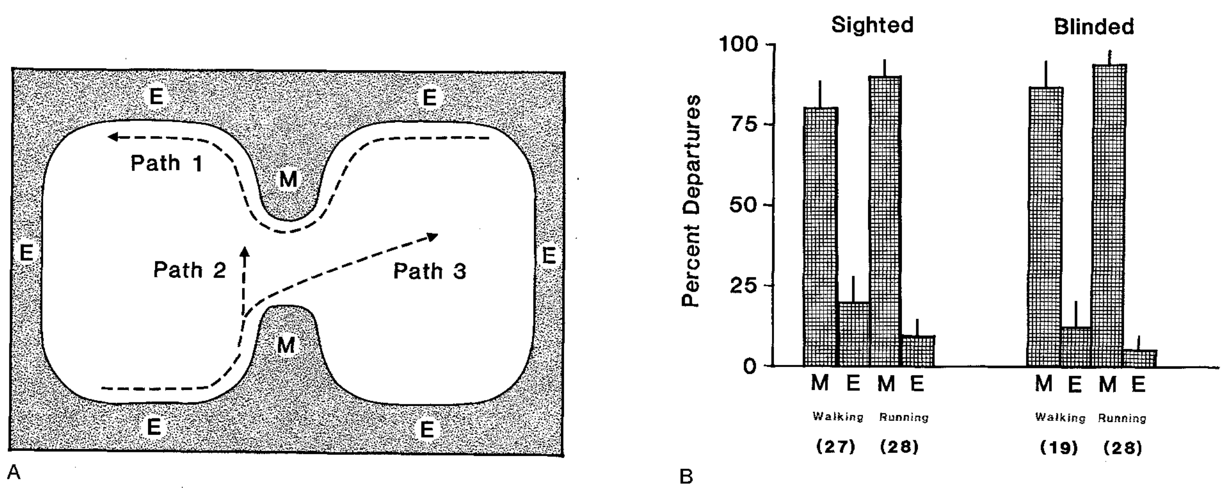


Figure 2. *A* Hourglass arena for distinguishing active vs passive wall-following. E = end, M = middle; paths 1, 2, and 3 are predicted for strongly active, passive, and weakly active wall-followers, respectively. *B* Patterns of American cockroach departures from the hourglass arena walls. M = departures from the convex curves at the middle of the arena, E = departures from straight or concave walls, bars in histogram are means ± 95% C.L. Numbers in ( ) = n. Values in histogram are NOT weighted in proportion to the lengths of wall which are convex vs concave and straight. Nine blinded cockroaches refused to move without stimulation, hence the reduced n for blinded, walking animals.

mental animal to prevent any trail following) which was laid on the floor (room temp. 19–23 °C). Balanced fluorescent lighting at 50-ft candles enabled videotaping of the animals' responses with a JVC BY-110 color video camera mounted from the ceiling.

In the hourglass arena experiments, an intact cockroach was gently released into the center of one of the arena ends (E, fig. 2 A) and allowed to walk about for 3–5 min. It was then stimulated to run several times by touches from a plastic ruler administered to the terminal abdominal segments or hind legs; thus we were able to evaluate the influence of velocity (walking vs running) on wall-following behavior. To evaluate the potentially confounding effects of visual response to a nearby wall on wall-following behavior, each cockroach was blinded by an application of Liquid Paper™ correcting fluid. After 30 min for acclimation to blinding, the propensity of each cockroach to depart from the hourglass arena walls while walking and running was again quantified. A total of 28 cockroaches was tested. Each cockroach was exposed to each of the four treatments. Wanting to minimize the effect of handling on the animals' behavior, we did not randomize the order of treatments, i.e., sighted animals were tested before being blinded; the effect of walking was assessed before running. A departure was scored when an animal moved more than 1 antennal length from the wall and did not return to a nearby section within ca 1 s. Departures were recorded from all locations along the arena wall. The vast majority of departures led to recontacts with non-adjacent walls. Typewriter correction fluid used for blinding did no apparent damage, as 9 cockroaches retested after having their blinders peeled off behaved no differently in the hourglass arena than before blinding.

The effect of wall curvature was tested with a Chi-square test on departure data weighted by the relative lengths of wall for M and E. Expected departures were determined by dividing the total number of departures by the total wall length (330 cm) to obtain the number of departures/cm. This value was then multiplied by the lengths of the convex (62 cm) and concave and straight walls (268 cm) to give the expected number of departures if the tendency for cockroaches to depart were equal for all walls. The effects of walking vs running and sighted vs blinded were tested using a G-test 2 × 2 contingency table[9].

Variable convex curvature experiment. To quantify the thigmotactic tendency of American cockroaches more precisely, animals were stimulated to run along a 40-cm straight wall of flexible plastic which thereafter was arranged into curves of varying radii [2, 20, 40 and 80 cm, and infinity (= straight wall)]. To generate a percent departure datum, a given cockroach was run 5 times for each curvature. Seventeen cockroaches were tested on each curve; curves were presented in a random order. We elected to evaluate the response of only running cockroaches since there was little difference in departures for running vs walking animals in the hourglass arena trials.

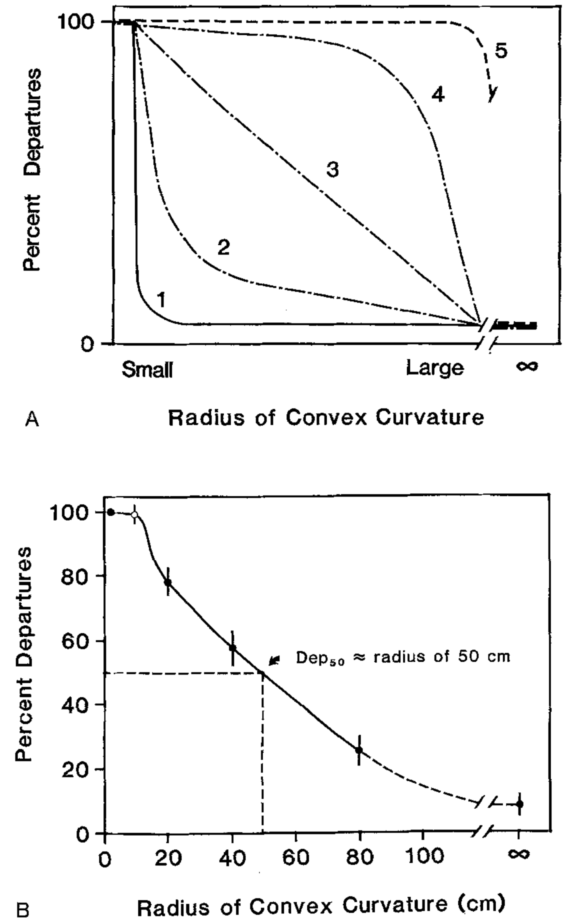


Figure 3. *A* Predicted responses of animals displaying varying degrees of wall-following on a range of convex curves. A near perfect wall-follower (curve 1) would rarely depart until perhaps the radius of curvature becomes so small relative to body size that the animals momentum guarantees departure. A straight-running passive wall-follower (curve 5) would always depart from convex curves until they became so gradual as to virtually parallel the animal's straight path. Hypothetical curves 2, 3 and 4 are suggested for strong, moderate and weak wall-followers, respectively. The improbability of an animal being a perfect wall-follower at all times is acknowledged by elevating the curves slightly above the X axis. *B* Pattern of departures for American cockroaches running along convex curvatures of varying radii. Bars indicate 1 SE. The data point for curvature of radius 10 cm came from sighted, running cockroaches in the hourglass arena experiment (n = 20).

Environmental conditions were very similar to those for the hourglass arena experiment and the arena was again placed on a sheet of wrapping paper. These trials were not videotaped, however. The degree of wall-following displayed was evaluated with respect to the hypothetical response curves shown in figure 3 A.

Results

Hourglass arena experiment. Whether walking or running, sighted or blinded, cockroaches usually followed concave and straight walls but departed from convex walls (fig. 2 B). All comparisons of the number of departures that occurred along the walls of the middle (M) vs the end (E) of the arena were highly significant (χ^2 test, 1 df: walking, sighted – $\chi^2 = 353.6$, $p < 0.001$; running, sighted – $\chi^2 = 583.5$, $p < 0.001$; walking, blinded – $\chi^2 = 221.0$, $p < 0.001$; running, blinded – $\chi^2 = 602.6$, $p < 0.001$). Cockroaches followed the wall around the convex curvature (M) only 23 of 514 total passes. Running resulted in a small but significant increase in departures for sighted cockroaches only (G test, $G = 6.292$, 1 df, $p < 0.025$). Overall, running increased the percent of departures over walking by only 9% (mean of data pooled for sighted and blinded animals). While blinding increased departures for both walking and running animals, it resulted in a non-significant increase of only 6% (mean of data pooled for walking and running animals). Thus, while both running and being blinded increased departures, these effects were minor compared to wall curvature. These data do not support the belief that American cockroaches are strong wall-followers.

Variable convex curvature experiment. Departures increased with increasing severity of the curvature (fig. 3B), suggesting that American cockroaches are moderately thigmotactic (compare response curve to those in fig. 3A). The remarkable tightness of the data and the approximate linearity at the mid-range of the response curve suggest that an animal's propensity to wall-follow can be established with good precision by interpolation from data like those of fig. 3B, e.g. the Departure_{50} for our running *P. americana* was a radius of 50 cm (or ca 12 times body length).

Discussion

We have demonstrated that moving American cockroaches are not as highly thigmotactic as was previously believed. Our results suggest that much of *P. americana's* reputation for being strongly thigmotactic was due to passive, barrier-directed wall-following (pseudothigmotaxis). Within the context of the framework presented in figure 3A, this species appears to be moderately thigmotactic. While there was little difference in the response of running vs walking animals in the hourglass arena experiment, it is possible that the response curves for walking and running cockroaches might diverge over the range of convex curvatures used in the second experiment.

The fact that vision did not strongly affect the pattern of departures (fig. 2B) supports the idea that wall-following in the American cockroach is primarily a response to tactile stimuli. Indeed, cockroaches moving along concave and straight walls almost always dragged an antenna along the wall. When cockroaches lost contact with a convex wall they often veered in the direction of the last antennal contact, but such turns were neither sharp enough nor quick enough to keep the majority of the animals in contact with convex walls having radii less than about 50 cm. This behavior of turning towards the side last stimulated is similar to the stereotropic response described by Crozier[3–5]. While this behavior could also be interpreted as idiothetic counterturning toward a previously favored course[2,10,11], it was not clear that cockroaches in our experiments had established any favored course other than that generated by wall contact. The mechanism underlying this turning behavior and whether its degree of development in various species correlates with the strength of a species' wall-following ability deserve further study.

The ideas and methodologies presented in this paper provide the first objective basis for: 1) distinguishing between active and passive wall-following, and 2) quantifying the intensity of active wall-following. Despite the convenience and tradition of using functionally concave behavioral arenas, future investigators of navigation by potential wall-followers must incorporate convex curves into their experimental arenas. Hopefully, this advance will help clarify both the extent to which animals actively follow boundaries in their environments and the possible importance of this behavior in foraging, homing and escape.

Acknowledgments. We thank T. Mowry and J. Keller for help in conducting these experiments, and Prof. R. Hollingworth for the cockroaches. Reviews by R. Cowles, F. Dyer, J. Keller, M. McPeek, T. Mowry and J. Spencer improved the manuscript. Contribution number 657 of the Kellogg Biological Station. This paper is dedicated to the memory of Dr Daniel Franklin Milam.

1 Fraenkel, G. S., and Gunn, D. L., The Orientation of Animals: Kineses, Taxes and Compass Reactions. Dover Publications Inc., New York 1961.
2 Schöne, H., Spatial Orientation: The Spatial Control of Behavior in Animals and Man. Princeton University Press, Princeton, New Jersey 1984.
3 Crozier, W. J., and Moore, A. R., J. gen. Physiol. *5* (1923) 597.
4 Crozier, W. J., J. gen. Physiol. *6* (1924) 531.
5 Crozier, W. J., and Pincus, G., J. gen. Physiol. *10* (1926) 257.
6 Weston, P. A., Experimental and Theoretical Studies in Insect Chemical Ecology: Ovipositional Biology of *Delia* Flies and Simulation Modelling of Insect Movement, Ph.D. Thesis. Michigan State University, East Lansing, Michigan 1986.
7 Motyka, G. L., Merritt, R. W., Klug, M. J., and Miller, J. R., Can. J. Zool. *63* (1985) 1388.
8 Bell, W. J., in: The American Cockroach. Eds W. J. Bell and K. G. Adiyodi, pp. 371–397. Chapman and Hall, London 1981.
9 Sokal, R. R., and Rohlf., F. J., Biometry, 2nd edn. W. H. Freeman and Co., New York 1981.
10 Burger, M.-L., Z. vergl. Physiol. *71* (1971) 219.
11 Mittelstaedt-Burger, M.-L., in: Information Processing in the Visual System of Arthropods, pp. 275–279. Ed. R. Wehner. Springer Verlag, Berlin 1972.

0014-4754/90/070758-04$1.50 + 0.20/0