

HIGH-FREQUENCY STEERING MANEUVERS MEDIATED BY TACTILE CUES: ANTENNAL WALL-FOLLOWING IN THE COCKROACH

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Summary

Cockroaches (*Periplaneta americana*) use their antennae to detect a wall and to maintain a constant distance from it as they walk or run along it. The faster they run, the closer they position themselves to the wall. They also use their antennae to detect and follow multiple accordion-like projections in the wall. They can make up to 25 body turns s^{-1} for short periods during rapid running to follow such wall projections. Each turn apparently involves a change in stepping direction. These turns help to avoid collisions with the outward projections, while keeping the body close to the wall.

Sensory inputs from the flagellum of the antenna, and not from its base, appear to evoke the turns in response to wall projections. These flagellar inputs appear to report the position along the antenna of its contact with the wall and/or the position of the consequent antennal bend. This flagellar information constitutes a one-dimensional sensory map, with location along the map indicating the distance to the wall.

Key words: cockroach, *Periplaneta americana*, steering, antenna, avoidance behaviour, orientation.

Introduction

Animals that are behaviorally active under conditions of low light often use non-visual means to guide their locomotion. A common arrangement is the use of mechanoreceptors located on, or at the base of, anteriorly placed, filamentous structures, such as mammalian vibrissae or arthropod antennae (Ahl, 1986; Carvel and Simmons, 1990; Dreller and Kirchner, 1993).

The cockroach *Periplaneta americana* is nocturnally active. It has very long antennae (up to 1.3 times the length of the body), which it holds in a forward and slightly lateral position while it runs. This suggests that the antennae may help guide the cockroach's locomotion by sensing objects in its path. However, the cockroach's running can be very rapid, with stepping rates up to 25 s^{-1} and forward speeds up to 0.8 $m s^{-1}$ (Delcomyn, 1971). This raises the question of whether its antennae can actually provide tactile information rapidly enough to be useful in guidance or whether cockroaches run 'blind'. As this insect is legendary for its rapid and adroit escape maneuvers, we suspected that its antennal guidance of running might be highly developed. We show here that this is the case.

In this study, we take advantage of the cockroach's natural tendency to walk or run along a wall to test its antenna-based locomotory guidance, especially during fast running. Although little is known about this subject, it had been shown that touching an antenna of a standing cockroach often evokes an abrupt turn in the opposite direction. Cockroaches can use this tactile response to turn away and escape from some predators (Comer et al., 1994;

Camhi et al., 1978). Thus, antennal inputs can induce rapid turning responses of the body away from the stimulated antenna.

We suspected, however, that the cockroach might use its antennae in more complex ways than this to guide its running. For instance, when a cockroach is placed in an arena surrounded by a wall, it spends most of its time walking along the wall, which it touches with its ipsilateral antenna. In this situation, the contact of the antenna with the wall does not induce an escape turn, but rather appears to play a role in maintaining the cockroach's position relative to the wall. This appears, then, to be a different type of antennal response from that induced by contact with a predator, and a type that has not apparently been studied before (Ritzmann et al., 1991).

A cockroach's antenna is a highly segmented structure. In the adult male, there are 150–170 segments, each covered with hard cuticle, so that movement occurs only at the intersegmental folds. The antenna is subdivided along its length into two specialized basal segments, the scape and then the pedicel, followed by the flagellum, which makes up all the remaining, unspecialized segments. Although passive bending can occur between segments all along the flagellum, as when the antenna is bent as it contacts a wall or other object, muscle insertions occur only in the scape and pedicel. Thus, to move an antenna, the cockroach contracts these basal muscles, and the entire flagellum follows passively. In addition, there is a hemolymph pump in the head that directs hemolymph out

through a tubular vessel to the antennal tip, from which it returns through the antennal tissues (Pass, 1985). This pumping action is weak and does not produce any antennal movement. It is possible that this pump, together with the general hemolymph pressure in the head capsule, could contribute hydrostatic forces to control antennal stiffness (G. Pass, personal communication).

Six different types of mechanoreceptors or putative mechanoreceptors are associated with the cockroach antenna. Of these, three are located along the flagellum: the campaniform sensilla, the marginal sensilla and the mechanoreceptive cells of terminal-pore hairs (Shafer and Sanchez, 1973; Toh, 1977; Schaller, 1978; Seelinger and Tobin, 1982). Three different types are found on or within the pedicel and/or scape: mechanoreceptive hairs, chordotonal organs and Johnston's organ (Campbell, 1972; Schmidt, 1969; Shafer and Sanchez, 1973; Seelinger and Tobin, 1982). This spatial separation of two sets of mechanoreceptor types permitted us to study the separate contribution of each set in antennal guidance of locomotion.

We report here on the cockroach's orientation along walls of different configurations and the sensory basis of this orientation. We find that the cockroach controls its distance from the wall using its ipsilateral antenna. Moreover, when negotiating a pleated wall, one with accordion-like projections towards and away from the cockroach, the cockroach can follow these projections even while running at high speed, changing its body orientation so as to minimize wall collisions while maintaining general proximity to the wall. In fact, for brief periods, a cockroach can achieve up to 25 turns s^{-1} , a higher rate than we know of for any other animal. We present evidence that the antenna ipsilateral to the wall provides the sensory input for this response and that the key receptors are located on the antenna's flagellum and not at its base.

Materials and methods

We used adult male *Periplaneta americana* from our laboratory culture throughout this study. We raised the animals in 250 l plastic barrels. We cut holes in the lids and sides of the barrels and covered these with window screen. The barrels contained cardboard egg cartons to provide many small sheltered spaces. The animals were kept on a 12 h:12 h L:D cycle and were fed rat chow and water *ad libitum*.

We observed a cockroach's running behavior along a wall by placing it in a circular arena 1 m in diameter. The arena was surrounded by a wall of tin sheeting 12 cm high. We applied Vaseline to the upper two-thirds of the wall to prevent the cockroaches from escaping. One side of the circular arena was closed off by a tin 'observation wall' that formed a chord across the arena (Fig. 1A). We studied the running of the cockroach along this wall. The observation wall was either straight or pleated to give accordion-like projections, each triangular in shape (Fig. 1B). For most studies, we used a peak-to-peak distance between the multiple projections of 7.5 cm as shown, although for some observations we used a peak-to-peak distance of 11 or 15 cm. The projection depth was 2.2 cm in all

cases. Multiply pleated walls permitted us to observe the cockroach making a series of turns, but for the camera to capture such a series required working at low magnification.

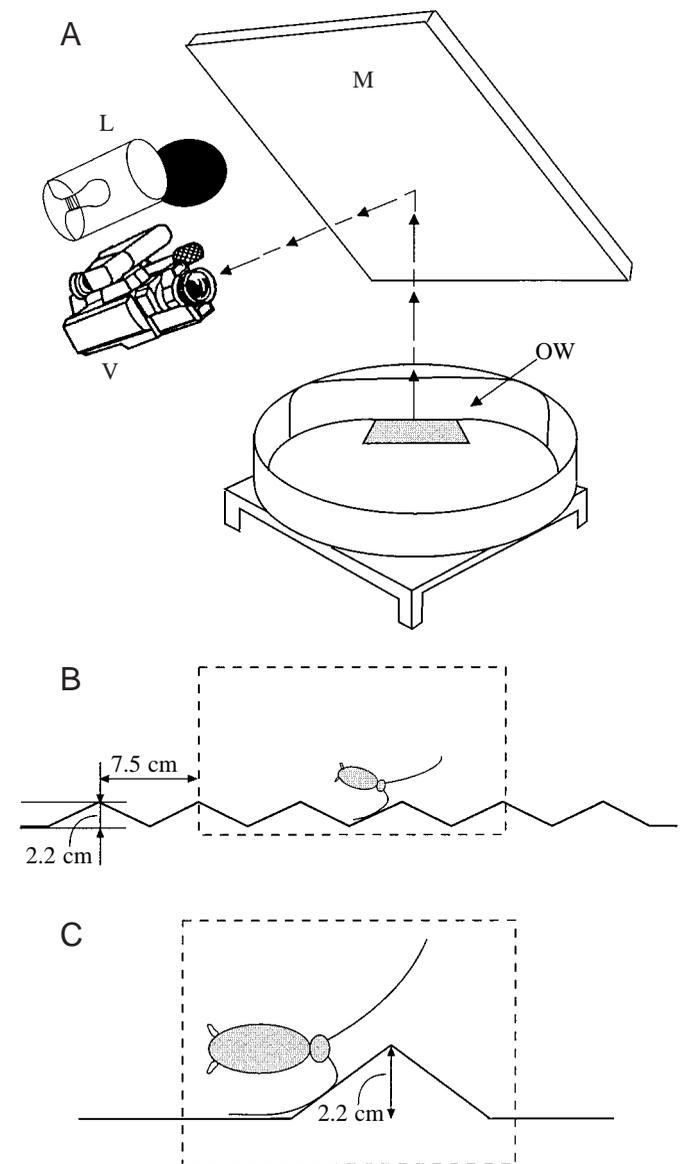


Fig. 1. Observational arrangement. (A) The high-speed video camera viewed through a 45° mirror a length of observation wall (OW) that formed a chord across a circular arena. For some studies, the observation wall was straight, as shown. The hatched rectangle in front of the observation wall indicates the approximate area of the camera's view. (B) For some studies, the observation wall was pleated, with multiple triangular projections of the dimensions shown, as seen from above and drawn to scale. The orientation in B and C is flipped, relative to that in A, so that here a turn away from the wall would take the cockroach upwards on the page. This is consistent with the graphical representations in the remainder of the figures; turns away from the wall are upward-going. The dashed rectangle indicates the approximate area of the camera's view. (C) Same as B, but with a single wall projection. In B and C, the cockroach's body plus head is 4 cm long and its antennae are 5 cm in length. V, video camera; L, lamp; M, mirror.

This caused a loss of some detail in viewing the antennae and tarsi (feet), which was important for some questions we asked. Thus, we made additional observations at higher magnification of the cockroach negotiating a single triangular projection in an otherwise straight wall (Fig. 1C).

We recorded the behavior of the cockroach using a high-speed video camera (NAC, Tokyo), at $250 \text{ frames s}^{-1}$, and analyzed the behavior frame by frame using the hardware/software package Movias (NAC), as described below. The camera's view was through a mirror above the arena, angled downwards at 45° . Linear resolution was 1–2.5 mm, depending on the magnification at the time of taping. We illuminated the arena with an 800 W lamp. We directed the light through the mirror, blocking the direct light path to the arena. We left the lamp on for the briefest intervals required for filming to avoid overheating. For a few recordings, we used a low-speed video camera (Sony Betamax, 24 frames s^{-1}) and illuminated the room with fluorescent lights plus a single 150 W incandescent bulb 1.5 m above the arena. Using the Betamax, we made measurements directly from the screen of the monitor with the tape in the pause mode.

For a given set of observations, we placed a single cockroach in the arena and waited for several minutes for it to become accustomed to the environment. The insect generally ran or walked along the walls of the arena, including the observation wall. We then turned on the lamp and camera and either waited till the cockroach ran along the observation wall or touched it lightly to induce running. We taped several such runs of each cockroach in either direction along the observation wall.

The cockroaches we used were either normal individuals or those that had undergone various treatments. All treatments were carried out under a dissecting microscope, using no anesthesia, on hand-held cockroaches. Unless otherwise stated, we allowed 1 day for recovery from the treatment before video-taping the behavior. The purpose of these treatments was to help to define the sensory basis of the cockroach's response to the wall and its projections. As baseline controls, we used both the runs of normal individuals and runs in which treated cockroaches ran with their untreated, control antenna towards the wall.

To remove possible visual inputs from the wall projections, we blinded one group of cockroaches by covering the compound eyes and ocelli with molten wax mixed with carbon black. For some of these animals, we also ablated the cerci to eliminate the possibility of air currents acting as a positional cue.

We carried out three types of antennal treatments. First, we ablated either all, or the distal half, of one antenna. Second, in a treatment designed to study the possible role of the mechanoreceptors associated with the antennal base in locomotory guidance, we fixed the basal part of one antenna in place by gluing it to the head capsule. As a result of this treatment, the scape, pedicel and roughly the first 10 flagellar segments of one antenna were covered with glue, as was part of the ipsilateral compound eye. While gluing, we arranged the antenna such that the flagellum pointed at an angle of $20\text{--}30^\circ$ lateral to the midline and slightly above the horizontal (the normal angle at which the cockroach holds the antenna while running).

We used two different glues for this treatment. One was Rubber Cement (Sanford) which, although slightly elastic, nevertheless held the antenna for well over a day. After drying, when we gave sharp taps to the flagellum that bent it by up to 90° , the antennal base moved by no more than approximately 2° , as viewed through a stereo microscope. The other glue was Superglue (Loctite). This held the antennal base completely rigid, such that even when we made sharp movements of the flagellum, no movement of the basal segments was visible, as viewed through a stereo microscope at $50\times$ magnification. However, since this glue remained intact for only a few hours, we studied these animals immediately after the glue had dried.

Immediately after the behavioral testing, we checked under the stereo microscope that the glue was still intact. Neither type of glue had any noticeable toxic or generally inimical effect on the antennal sensory apparatus. For instance, sharp tactile stimulation of an antenna evoked escape turns as in normal cockroaches (Comer et al., 1994). Also, these cockroaches generally maintained a normal range of distances from the straight wall while walking along it.

We carried out the third antennal treatment, which we call 'cut and paste,' to study the possible role of the mechanoreceptors associated with the antennal flagellum in locomotory guidance. We cut an antenna at a distance of 2 cm from its base, and then glued it back in place using Histoacryl glue (Braun, Melsungen, Germany). Before re-attaching the distal cut portion, we removed a short length of its proximal end, so that it would fit snugly inside the tapering proximal antennal portion. The treated antenna was, therefore, slightly shorter than its original length. To eliminate the possibility that the distal and proximal ends of the cut sensory axons might fuse (Bittner, 1988; Camhi and Macagno, 1991), we attempted to kill all tissues in the distal segment in a microwave oven, before re-attaching it. Even brief microwave treatments caused the flagellum to become brittle and to break readily. However, as we show below, axonal fusion cannot explain our results.

We analyzed video-taped data using the program Movias on a PC platform. For each video frame throughout a run, we entered into the program the positions of the wall and of several parts of the cockroach's body. For various types of observation, these included the midpoints of the head and of the rear end of the body, the tarsi of each of the six legs and several antennal positions. These latter included the antennal base and tip, the position where the antenna contacted the wall (which was not necessarily at its tip) and the estimated position, accurate to a few millimeters, where the antennal flagellum, which is straight as it leaves the head, began to bend in response to contact with the wall. This last point also permitted us to determine the angle between this unbent antennal base and the midline of the body. We also entered 15 additional points along the antenna, which we used to reconstruct its shape. These points, roughly equally spaced along the antenna, did not represent specific morphological landmarks. We found that this number of points accurately represented the smoothly varying shape of the antenna.

The program produced graphical analyses of several

parameters as a function of time and in relation to the cockroach's position relative to the wall projections. These parameters included body angle, the positions of each leg relative to the body, the shape and angle of each antenna and the position of the antennal bend and point of contact of the antenna with the wall.

Results

Cockroaches spent the great majority of their locomotory time walking along the wall. They either palpated the wall with the ipsilateral antenna or dragged this antenna along the wall as they walked. It was our initial impression that, the faster they walked, they more they tended to adopt a position closer to the wall. To quantify this, and to provide baseline data for studying their responses to wall projections, we first videotaped their locomotion along the straight observation wall, with no projections, using a magnification adequate to reveal the details of antennal contact with the wall. We tested intact cockroaches and those with half or all of one antenna ablated.

We subdivided the trials according to the cockroach's stepping rate, which we measured in the middle of the field of view, as fast (12–23 steps s^{-1}), medium (8–11 steps s^{-1}) and slow (1–7 steps s^{-1}). Under the bright light required for the high-speed video, the cockroaches seldom walked slowly along the wall, perhaps because of their negative phototactic tendency (Guthrie and Tindall, 1968). In fact, we recorded only 12 trials of slow walking data under these conditions (three in intact cockroaches, five with a half-ablated antenna and four with a fully ablated antenna). To supplement these slow-walking trials, we used the low-speed video, which required much less intense illumination. Since it was not possible to measure stepping rate accurately with the low-speed video, the leg movements being poorly resolved, we only accepted as slow walking trials those in which it was clear by visual estimation that the cockroach stepped at close to its normal walking rate of 3–4 steps s^{-1} and walked in brief bouts separated by brief pauses, its normal mode of slow, exploratory walking (Gras et al., 1994).

For each trial, we measured the shortest distance from the midpoint of the head to the wall. Since the cockroach generally ran with its body parallel to the wall, changes in distance from head to wall reflect changes in distance of the whole body from the wall. For fast running trials, we accepted for analysis trials only in which the cockroach did not stop running while in the camera's field of view.

In the majority of trials, the cockroach remained at a remarkably fixed distance from the wall, the head-to-wall distance varying by no more than a few millimeters during the video-taped run. However, there were a small number of trials in which the cockroach clearly ceased relating to the wall in mid-run and entered the open space in the middle of the arena. To eliminate such trials from the data pool, we adopted the criterion, for all locomotory speeds, that if the distance from the head to the wall changed by more than ± 1 cm, from the moment the head entered till it left the field of view, we rejected the trial. This was the case in less than one-quarter of all trials.

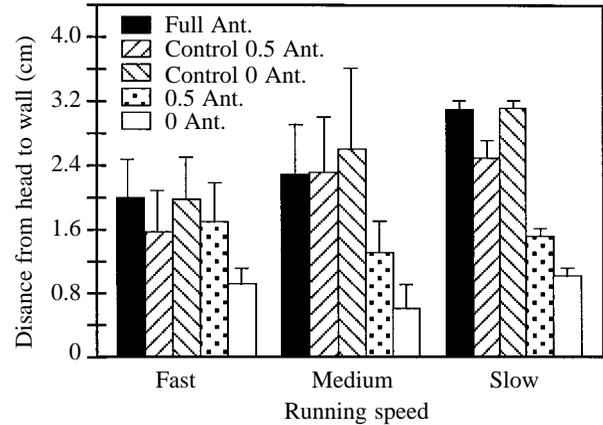


Fig. 2. Distance from the cockroach's head to the wall under different experimental conditions. Full Ant., normal cockroaches, which walked with either intact antenna along the wall. Control 0.5 Ant. and Control 0 Ant., trials in which cockroaches walked with their normal, intact antenna towards the wall and their treated antenna (half ablated or fully ablated, respectively) away from the wall. 0.5 Ant., trials in which cockroaches walked with an antenna that had been cut to half its length along the wall. 0 Ant., trials in which cockroaches walked with the side of their fully ablated antenna along the wall. Each group of cockroaches included between 9 and 13 individuals. The numbers of trials in each category are as follows, for the 15 columns shown, reading from left to right on the graph: Fast, 27, 13, 17, 15, 24; Medium, 14, 12, 8, 11, 4; Slow, 40, 29, 42, 30, 40. Of these slow walking trials, the following numbers were filmed using the high-speed video: 3, 0, 0, 5, 4; the remaining trials were all filmed using the low-speed video (see Materials and methods). Column heights are means, and bars show one standard error of the mean (S.E.M.).

In general, the faster an intact cockroach ran, the closer it appeared to position itself to the wall. This was true both for the intact cockroaches (Fig. 2; compare the three black columns) and for cockroaches with one treated antenna, but running with their untreated, control antenna against the wall (Fig. 2, compare the three positive-slope or the three negative-slope hatched columns). The difference appears to be greatest between slow-running and medium-running trials. A Kruskal–Wallis test carried out for the three black columns rejects the null hypothesis that there is no difference among these three data sets ($P < 0.001$). The same test produced the same result both for the three positive-slope hatched columns and for the three negative-slope hatched columns.

Whenever a cockroach begins to walk or run, it immediately positions each antenna in front of the body, at an angle of approximately 30° to the body's midline. For an adult male of 4 cm body length, whose antennae are nearly 5 cm in length and typically include a slight lateral arch from base to tip, the two antennae cut a sensory swath approximately 5.5 cm wide. This is wider than the distance between the outermost points on the left and the right legs (typically approximately 4.0 cm). Thus, the antennae could well alert the cockroach to an obstacle with which its legs or body are about to collide. Cockroaches also hold their antennae at a similar angle while

walking along a wall and often touch the wall with the ipsilateral antenna. This could provide a possible sensory basis for determining the location of the wall relative to the body and thus of controlling distance from it.

The percentage of time for which the antenna was in contact with the wall varied with running speed, being $73 \pm 32\%$ (mean \pm S.D.) for fast running and $49 \pm 32\%$ for medium-speed running. This difference was significant ($P=0.034$, Mann–Whitney two-tailed test). For slow stepping, we could not resolve on the low-speed video the times of antennal contact. However, visual inspection indicated that the cockroaches made only brief, intermittent taps, both while they were walking slowly and during pauses between walking bouts. In general, then, the faster the cockroach runs, the greater the percentage of time it is in contact with the wall.

To help indicate whether antennal contact with the wall does provide the sensory information to control body position, we measured the distance maintained by cockroaches that ran with the half-ablated or the fully ablated antenna ipsilateral to the wall. In general, the shorter its antenna, the closer the cockroach walked to the wall. For instance, when running at slow or medium speed, cockroaches remained closer to the wall when their half-length antenna, rather than their opposite intact antenna, was towards the wall [Fig. 2; compare, for medium and slow speeds, the stippled and positive-slope hatched columns; this effect was highly significant for slow and medium running ($P < 0.001$ and $P = 0.006$, respectively) but was not significant for fast running ($P = 0.95$), where the cockroaches in control trials already ran close to the wall; Mann–Whitney two-tailed test]. When walking with a fully ablated antenna next to the wall, this effect was even greater (Fig. 2; compare, for each running speed, the open and negative-slope hatched columns; this effect was highly significant for all running speeds; slow, $P < 0.0001$; medium, $P = 0.004$; fast, $P < 0.0001$; Mann–Whitney two-tailed test). Also, animals walking with a fully ablated antenna next to the wall walked closer than those with a half-ablated antenna next to the wall (Fig. 2, compare open and stippled columns, for each running speed). This was significant for all running speeds (slow, $P < 0.0001$; medium, $P = 0.016$; fast, $P = 0.004$; Mann–Whitney two-tailed test). When the animals walked particularly close to the wall, there was an increased tendency for their legs and pronotum to contact the wall. We did not attempt to quantify this. It appeared, however, as though, in the absence of antennal input, the cockroach was using receptors on these other body parts to maintain a relatively fixed, although now closer, position relative to the wall.

It appears that, for a given running speed, the more of an antenna one removes, the closer the cockroach remains to the wall. We confirmed this by comparing, for each running speed, intact cockroaches (black columns in Fig. 2) with half-ablated (stippled columns) and fully ablated (open columns) using a Pearson correlation. The correlation was significant for all running speeds (slow, $P < 0.001$; medium, $P = 0.03$; fast, $P < 0.0001$). We will return to the question of antennal mediation of responses to the wall after describing the cockroach's response to wall projections.

Given that the cockroach maintains rather tight control of its distance from the wall, what happens if the wall bends outwards, towards the cockroach, or inwards and away from the cockroach, as in our triangular wall projections? Fig. 3A

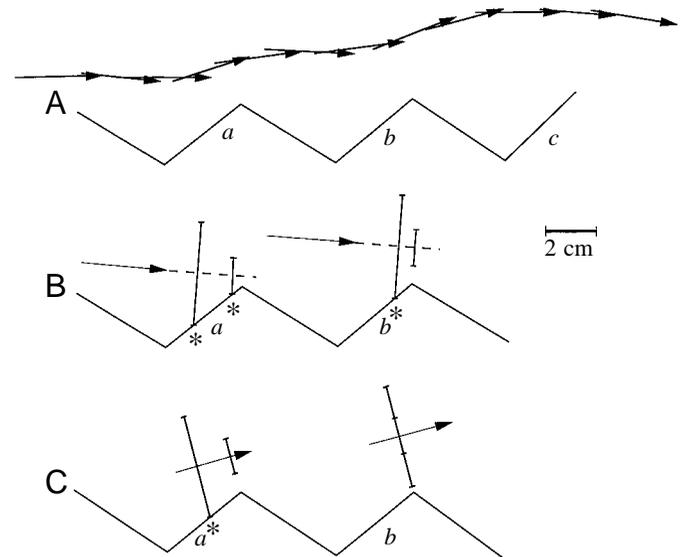


Fig. 3. The turning responses of a running cockroach to wall projections. (A) The accordion-shaped line across the bottom represents the wall. Each arrow's length represents the cockroach's body length, and its position and angle represent those of the body at a given instant. The time separation between arrows is 40 ms (every tenth video frame shown). The first arrow represents 20 ms after the entire body became fully visible to the camera. The cockroach's right antenna touched the outward wall projection labeled *a* at approximately the time represented by the first arrow and touched the outward projection labeled *b* at approximately the time represented by the sixth arrow. These times are quantified in Fig. 4A. The antenna did not touch the outward projection labeled *c* and, correspondingly, the cockroach did not turn outwards. (B,C) Analysis of the outward turns from walls *a* and *b* in A. (B) The two arrows shown are the second and the sixth arrows from A, when the cockroach was heading most sharply towards the wall. The broken line in front of each arrow shows the trajectory that would have occurred if the cockroach had not turned outwards, but rather had continued straight along the path of the arrow. The two lines perpendicular to this broken line mark the width of the cockroach; the longer line marks the estimated outermost width of the legs (4 cm), and the shorter line marks the width of the body itself (1.3 cm). Each of these 'width markers' is drawn at the point where the legs or the body, respectively, would have collided with the wall, had the cockroach not turned; if the cockroach would not have collided with the wall, the width marker is drawn adjacent the outer tip of the wall projection. Prospective collisions are shown by asterisks. (C) The two arrows shown here are the fourth and the eighth arrows from A, when the cockroach had turned most strongly away from the wall. On the basis of this angle of turn, we calculated geometrically the expected wall collisions. Only one collision is expected, namely, that by the legs against wall segment (*a*). In fact, this predicted collision, and only this one, did occur, as shown in Fig. 4A. However, it occurred later and closer to the outer tip of the wall projection than shown in Fig. 3C, indicating that the cockroach's evasion was even more effective than predicted.

shows the turning responses of a cockroach to a sequence of such projections. The peak-to-peak distance of these projections was 7.5 cm. The cockroach was running at a stepping rate of 15 s^{-1} . As the arrows show, the cockroach began by turning inwards towards wall segment *a*, then turned outwards from *a*, inwards towards *b*, outwards from *b* and inwards towards *c*. Although the angular shifts appear small, such turns can be effective in significantly reducing the number of collisions with the wall that would have occurred had there been no outward turning (Fig. 3B,C).

Fig. 4A quantifies the turning responses from the run shown in Fig. 3. At the times shown by the two open arrows in Fig. 4A, the antenna contacted the first two outward wall projections, *a* and *b* in Fig. 3. Each contact was followed by an outward turn (upwards in Fig. 4A). The antenna did not contact the third outward wall projection (*c* in Fig. 3) and, correspondingly, there was no third outward turn. Following

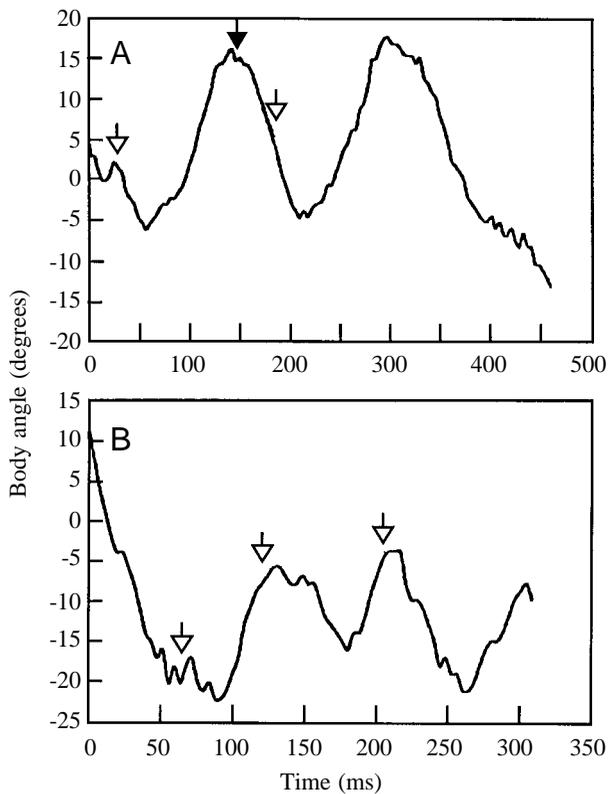


Fig. 4. Body angle relative to the wall as a function of time for two runs along pleated walls. 0° corresponds to the body's long axis being parallel to a line connecting the outermost points of the wall projections (e.g. the uppermost points of the wall in Fig. 3A). Upward deflections represent turns outwards from the wall; downward deflections, turns towards the wall. Open arrows show the onset times of antennal contact as the cockroach approached each projection. The filled arrow shows the moment of leg contact with the wall. (A) Same run as in Fig. 3. (B) A different trial, in which a different cockroach was running faster. It did not contact the wall with its legs or body, only with its antenna. Each of the three onset times of antennal contact (open arrows) corresponds to the subsequent outward turn (upward deflection). The second and third antennal contacts occurred before the end of the prior outward turn.

each outward turn, the antenna lost contact with the wall (not shown) and the body turned inwards again. The legs briefly contacted the outermost part of the first wall projection (filled arrow in Fig. 4A).

The turning angles on this trial were approximately 20° . The cockroach did not run away from the wall, into the center of the arena, but rather acted as though it was attempting to remain close to the wall, while avoiding collisions with its outward projections. In so doing, it made a total of four turns, left or right, within the period from approximately 80 to 380 ms, giving a mean turn duration of 75 ms or a mean turning frequency of 13.3 s^{-1} , approximately one turn per 1.1 step cycles.

Fig. 4B shows a trial by a different cockroach that was running faster, stepping at 23 s^{-1} . This run included a total of six turns in 300 ms or a mean turning frequency of 20 s^{-1} . In fact, because the initial part of this run involved a turn of long duration, if one considers only the interval from 100 to 300 ms, there were five turns in 200 ms, giving a turning frequency of 25 s^{-1} . This was among highest turning frequencies we encountered. During this 200 ms period, this cockroach was making approximately 1.1 turns per step cycle. Although these turns were small (mean 15° , excluding the initial 100 ms), the cockroach managed to avoid all contact between its legs and body and the wall.

We also made some observations of turning responses to less closely spaced wall projections, 11 and 15 cm peak-to-peak. Cockroaches were no less able to follow these wall projections. Since we were interested in observing the turning behavior near the limits of its performance, we made most of our observations at the 7.5 cm separation distance, which generally gave higher turning frequencies.

Cockroaches did not always succeed in following every cycle of inward and outward projections (e.g. Fig. 3A, wall projection *c*). In fact, out of 229 outward wall projections, the cockroaches turned outwards in response to 111 or 48%. There were several possible causes for these cases of no turn, one being the lack of antennal contact with the wall, which we discuss below. In evaluating the frequency of the cockroach's turning during a run, the absence of a single turning response would greatly reduce its apparent turning frequency, even though it might have responded to each of several other wall projections without fail and at a high frequency. Therefore, we expressed the turning capability of the cockroach in terms not of mean turning frequency for each run, but as the duration of each individual inward and outward turn (including those in which it missed a cycle, which were generally of longer duration). We obtained these data by measuring the duration from trough to peak, from the same peak to the next trough, from the same trough to the next peak, etc., for each turn, based on graphs of the type shown in Fig. 4A,B.

A histogram of durations of both inward and outward turns (Fig. 5A) shows that durations as brief as approximately 50 ms were not uncommon. Those as brief as approximately 30 ms occurred occasionally. It should be noted that a series of 50 ms turns would give a turning frequency of 20 s^{-1} , which is within

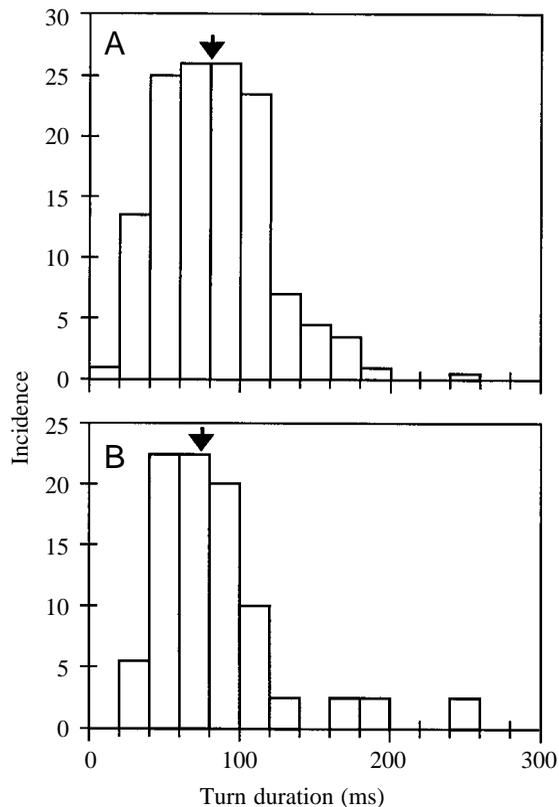


Fig. 5. Durations of turns in response to outward and inward wall projections. (A) Data from all turns. (B) Data only from turns outward from the wall. Arrows show mean turn durations.

the range we observed. A series of 30 ms turns would give a turning frequency of approximately 33 s^{-1} . We never observed such a high frequency of turning and, given the distributions plotted in Fig. 5A, this would seem to be approximately the cockroach's maximum possible frequency. These observations suggest an extremely rapid rate of body turning in response to sensory input.

One might assume that the briefest turns in Fig. 5A would be inward turns, since these would be terminated in response to the antenna contacting the wall. However, analysis of outward turns only (Fig. 5B) shows these to be similar to all turns together.

We quantified the turn size for outward turns only in response to outward wall projections (Fig. 6), since inward turn size would be influenced by the next antennal contact with the wall. We analyzed only those responses that were preceded by an antenna touching the wall (i.e. where there was no leg or body contact with the wall until at least after the turn had been completed; as in the example shown by the one filled arrow in Fig. 4A). The mean turn size was $25.1 \pm 11^\circ$ (mean \pm s.d., $N=41$).

Given that the cockroach appears to use its antennae to regulate its distance from a smooth wall (Fig. 2), and given that it makes inward and outward turns in accordance with wall projections, we presumed that antennal detection of these projections might also evoke the cockroach's turning response.

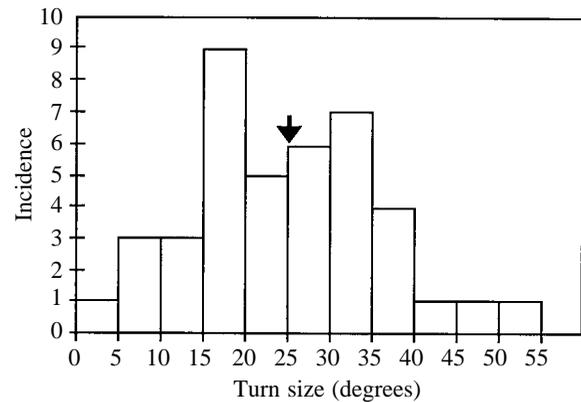


Fig. 6. Sizes of outward turns in response to outward wall projections. The arrow shows the mean value.

To test this, we first re-examined the turning responses of cockroaches to multiple wall projections to determine whether examples in which the cockroach did not turn outwards from an outward projection were correlated with the antennae not having touched the projection.

The cockroaches ran past a total of 55 outward projections that they did not touch with antennae or legs. For only four of these (7%) did the cockroach turn outwards prior to arriving at the subsequent outward projection. The mean size of these four turns was $13 \pm 2^\circ$ compared with 20° for those when they did contact the projection. In contrast, the cockroaches ran past a total of 174 outward projections that they did touch with the antenna ipsilateral to the wall. For 107 of these (61%), they initiated an outward turn prior to contacting the projection with the legs or body. The difference between 7% and 61% was highly significant ($P < 0.0001$; Fisher's two-tailed test).

Further support for the idea that the antennae mediate the turning response to a wall projection came from tests on three cockroaches whose compound eyes had been covered with black wax and whose cerci had been ablated. Two days after this treatment, we video-taped the responses of these cockroaches as they ran past multiple wall projections. These cockroaches appeared completely normal in terms of their locomotory coordination and their general behavior; however, their running speeds were lower than normal ($8.1 \pm 1.2\text{ steps s}^{-1}$, mean \pm s.d.; range $5.0\text{--}9.3\text{ steps s}^{-1}$) as measured from the video. We video-taped 25 trials in which the ipsilateral antenna contacted an outward wall projection. In 23 of these trials (92%), the cockroach made an outward turn. This is a higher percentage response than in normal cockroaches (61%). This may be due in part to the low mean running speed of these cockroaches, owing to which more time was available to start a turn, prior to colliding with the wall projection. The turn size was $21 \pm 8^\circ$ (mean \pm s.d.), consistent with those of intact cockroaches (mean 20°).

When a running cockroach approaches the outward projection, presumably what the ipsilateral antennae would sense is the decrease in distance between itself and the wall. To help determine what antennal cues the cockroach might use to detect this decrease, we filmed the cockroach's interaction with single outward projections at high magnification.

Fig. 7 shows the shape of the antenna ipsilateral to the wall on a single run, at 4 ms intervals, starting at the moment it first touched the outward projection. The cockroach was running from left to right at 14 steps s^{-1} . Prior to the time when the antenna first touched the outward projection, it had briefly touched the straight part of the wall and then, for a period of 68 ms, lost contact with the wall. Nevertheless, the antenna retained a slight bend near its tip until the onset of contact with the wall projection. The last antennal image shown was 12 ms after it lost contact with the tip of the projection. We will now describe this example in detail and then consider all the trials we studied.

The mere presence or absence of antennal contact cannot explain the turning response to a wall projection, since cockroaches running rapidly along a straight wall generally make nearly continuous antennal contact without this inducing any detectable outward turns. Two different candidates for the sensory cue evoking the turn can be seen in Fig. 7. First, as the cockroach approaches the outward projection, the straight portion of the antenna, from the cockroach's head to the start of the antennal bend, shortens. Second, as the cockroach approaches the projection, the location of the point along the antenna that is actually in contact with the wall moves proximally. The distinction between the location of the antennal bend and the point of contact with the wall can be seen most clearly late in the run, where the antenna contacts the projection near its tip, yet the bend is considerably more proximal. Each of these two parameters is represented as a one-dimensional map along the length of the antenna. A third candidate parameter is the angle of the antenna with respect to the head. A fourth candidate, the length of the antennal segment in contact with the wall, appears to be unsuitable, because a variable length of flagellum near the tip is often out of contact with the wall. This is hinted at in Fig. 7.

Fig. 8 analyzes the first three parameters in greater detail, for the same trial as shown in Fig. 7. Fig. 8A shows the body angle as a function of time; the open arrows indicate the times of onset and loss of antennal contact with wall projection (the former was the time of the first antennal image shown in

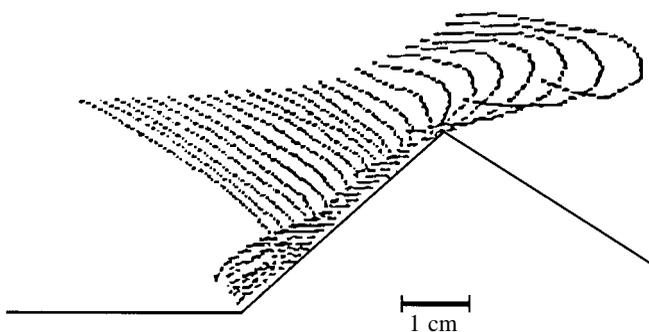


Fig. 7. Shape of the antenna ipsilateral to the wall, from the moment it first touched the outward wall projection until 12 ms after it lost contact with this projection. The cockroach was moving from left to right. Antennal images are separated by 4 ms. See text for further explanation.

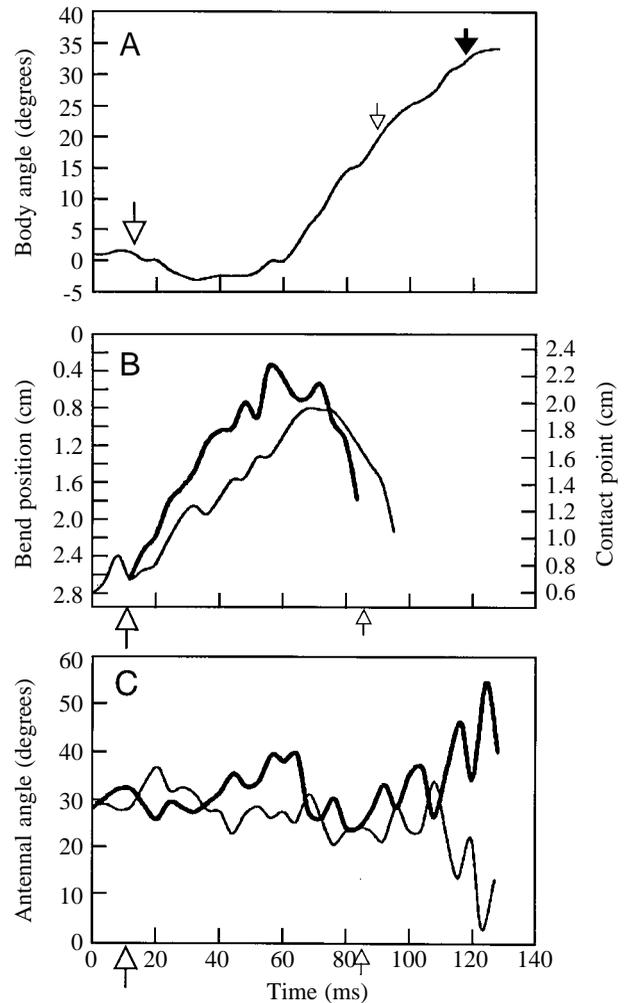


Fig. 8. Effects of an outward wall projection on a cockroach's ipsilateral antenna. Data from the same trial as in Fig. 7. (A) Quantification of the body turn. For this and the other parts of this figure, the large open arrow shows the time of onset of antennal contact with the wall, the small open arrow shows the moment when antennal contact was lost, and the filled arrow shows the time of leg contact with the wall projection. (B) Positions of the bend in the antennal flagellum (fine line) and of the point of contact with the wall (thick line). To obtain the most accurate data from the curved flagellum, we measured bend position relative to the antennal base and contact point relative to the antennal tip. Thus, the scale of bend position descends, the values decreasing with time, whereas the opposite is true for contact position. (C) Angle of the ipsilateral antenna to the head throughout the run. 0° represents forward, parallel to the head's anterior-posterior axis. An upward deflection indicates a backward movement relative to the head. Fine and thick lines as in B

Fig. 7). The latency from the time of antennal contact (large open arrow) to the clear onset of an outward turn in this trial was 45 ms. For all 22 trials, the latency was 29 ± 18 ms (mean \pm s.d.). Fig. 8B plots the position of the antennal bend and of the point of contact with the wall throughout this run. The former was measured as the length of the straight line from the antennal base to the point where the bend began, which was

readily definable in every trial. The point of contact was measured as the distance from the midpoint of contact to the distal tip of the antenna. In eight of the 22 trials, the distal end of the antenna was curved, complicating this measurement by our program. Thus, we did not measure the point of contact on these trials.

Not surprisingly, these two parameters parallel one another quite closely. In fact, both parameters contain information that could evoke not only the turn away from the wall as the cockroach approaches the outward projection (upward deflection of each curve) but also the reverse turn, as it comes to the tip of the wall projection (downward deflection of each curve after approximately 70 ms). Moreover, either of the two parameters plotted could potentially give a fairly accurate measure of the distance from the body to the wall, since the cockroach holds its antenna at a reasonably fixed angle relative to the body.

The angle of the antenna to the head was a third candidate parameter that could, in principle, inform the cockroach about the wall. That is, as the wall projection is encountered, it would push the antenna to a different angle relative to the head, a change that could presumably be detected by the mechanoreceptors of the scape and pedicel. However, it is not clear *a priori* that this parameter would be well-suited to all situations. When encountering a wall projection, one might expect the wall to push the antenna forwards or backwards or neither, depending on the angle of the antennal flagellum to the wall and, perhaps, the degree of wall friction. In the example shown in Fig. 7, the antenna strikes the projection at an angle close to 90° and, as the cockroach moves forward, the separate images of the antenna remain parallel to one another for at least the first 12 images, during which time information about the approach to the wall was presumably being acquired.

In fact, as shown in Fig. 8C, from this same trial, the angle of the antenna ipsilateral to the wall, with respect to the head, made mostly small fluctuations. These included no clear signals of opposite sign, properly timed for initiating, respectively, the outward and the subsequent inward turn of the body. We made similar plots for five trials from three different cockroaches and found no clear evidence of an angular signal resulting from contacting the wall. Thus, antennal angle does not appear to provide clear information about the wall projection.

We examined the position of the antennal bend in 22 trials for nine cockroaches and the position of the antennal contact in 14 of these trials (eliminating from the latter measure those trials in which the antennal tip was curved). Both the bend and the contact point moved proximally on all trials. The former began to move at a mean time of 5 ms, and the latter at 3 ms, after the moment of antennal contact with the outward wall projection. Since the sampling rate was every 4 ms, the true time at which these signals began to move could have been earlier than these values of 5 or 3 ms. This suggests, then, that one or both of the two signals from the antennal flagellum may provide the cue to induce a change in body angle.

A further group of cues that could possibly evoke the turn

concern the shape of the local bend caused by the wall projection rather than its location along the antenna. These could include the radius of curvature of the antennal bend, the length of antenna that lies flat along the wall and other factors. We did not attempt to quantify these; our general impression is that they are more variable than either bend position or contact position.

There is an enigma, however, in this suggestion that flagellar, rather than basal, sensory cues from the antenna may signal the wall projections. Given that the cockroach can respond very quickly to the outward wall projection (the mean latency from antennal contact to the start of the outward turn was 29 ms), the neural processing time must be quite short. However, as the antennal sensory axons are necessarily of small diameter (the antennal nerve serves over 270×10^3 sense cells; Schaller, 1978; Seelinger and Tobin, 1982), the presumably slow spike conduction velocity along most of the length of the flagellum would seem to be at odds with the requirement of a short processing time.

As one possible solution, even a very slight deflection in either direction, or merely a low-amplitude vibration, of the antennal base should be detectable by Johnston's organ (Kirchner, 1994) and perhaps by the other mechanoreceptors of the scape and pedicel. These may somehow signal both the presence and the direction of a wall projection. To test this, we carried out manipulations on the base and the flagellum of the antenna to determine which is the more involved in sensing the wall projections and inducing the turns.

We compared the behavioral responses of two groups of cockroaches to contact with single outward wall projections, which we filmed at high magnification. In the first group, we glued the base of one antenna in a fixed position; in the second, 'cut-and-paste' group, we cut off an antenna and glued it back in place (see Materials and methods). If flagellar receptors dominate the sensory input for the turn, then reasonably normal turning should occur following gluing that leaves the flagellum intact, but not following the cut-and-paste treatment, which severs the antennal nerve proximal to the points of both wall contact and antennal bend. In contrast, if basal receptors dominate, reasonably normal turning should occur following the cut-and-paste treatment, which should preserve both fairly normal movement of the antennal base and any vibrational information that may arrive there as a result of wall contact; but turning should not occur following gluing of the base, which should severely dampen any mechanical signals arriving at the scape and pedicel.

We glued with Rubber Cement one antenna in each of five cockroaches and video-taped 48 runs, in 35 of which the cockroach ran with its glued antenna towards the wall. Of these 35 experimental trials (Table 1, treatment 1), 63% (22 trials) showed an outward turn that began before the legs or body touched the wall projection. For these turns, the latency from antennal contact to the onset of the turn was 34 ± 11 ms (mean \pm S.D.), and the turn size was $28 \pm 13^\circ$. On the remaining 13 trials, in which there was no turn, the cockroach collided with the wall 55 ± 14 ms after antennal contact with the wall. These

Table 1. *The effect of various treatments administered to one antenna, each compared with the untreated contralateral antenna as its control, on various parameters of outward turns*

Treatment	N	Response (%)	Latency (ms)	Turn size (degrees)	Latency to collision (ms)
1 R. Cement	35	63	34±11	28±13	55±14
2 Control	13	69	31±4	33±12	54±8
3 S. glue	23	70	28±13	25±11	42±25
4 Control	19	79	32±13	34±14	37±4
5 S. glue + wax	16	63	29±12	19±11	37±11
6 Control	5	100	32±3	27±8	–
7 Cut + paste	10	0	–	–	54±26
8 Control	13	69	42±12	29±10	62±21

All responses are to a single outward wall projection.

R. Cement, Rubber Cement; S. glue, Superglue; S. glue + wax, Superglue on the antennal base and the head waxed to the pronotum; Cut + paste, antenna cut and glued back in place.

See text for further explanation.

Values are means ± S.D.; N is the number of trials.

turning responses were fully within the range of those from intact cockroaches.

To compare these turns with their controls (13 runs of the same cockroaches in which the untreated antenna was ipsilateral to the wall; Table 1, treatment 2), 69% (nine trials) gave outward turns. The latency was 31±4 ms (mean ± S.D.), and the turn size was 33±12°. In those trials where the cockroach did not initiate a turn before colliding with the wall, the latency from antennal contact with the projection to collision with the projection was 54±8 ms. These values were not significantly different between the experimental and control runs (percentage response, Fisher's exact test, two-tailed; other parameters, Mann-Whitney test, two-tailed; $P > 0.22$ for all comparisons).

The same appears to be true with Superglue, which we tested on five cockroaches (Table 1, treatments 3 and 4; no significant differences; $P > 0.08$ for all comparisons). This suggests that gluing the antenna in place does not significantly alter the cockroach's response to the outward wall projection, even though movements of the antennal base are all but prevented by this treatment.

It was possible, however, that antennal contact with the wall caused the head to move relative to the prothorax and that this movement was sensed by neck receptors that then induced the turning behavior. To test this, in a group of five cockroaches, we Superglued one antenna at its base and also waxed the head to the prothorax, preventing the head from moving. These cockroaches made completely normal turns, with no statistical difference between the two sides (Table 1, treatments 5 and 6; $P > 0.39$ for all comparisons).

We used three 'cut-and-paste' cockroaches to test whether removing sensation from the distal half of the antenna affects the behavioral response to wall contact (Table 1, treatments 7 and 8). Strikingly, there were no turning responses to contact with the wall when the 'cut-and-paste' antenna was ipsilateral to the wall, even though plenty of time was available for such

turns (a mean of 54 ms from the time of antennal contact till the body collided with the wall projection). In contrast, turning responses were normal in every way when the intact, control antenna was ipsilateral to the wall. The difference in the percentage response between the cut-and-paste' and the control cockroaches was highly significant ($P = 0.001$). Although we did not employ microwave treatment of the distal antennal segment to prevent axonal fusion, as explained in the Materials and methods section, the results indicate that this treatment was not essential. For even if fusion did occur, it would be difficult to explain how this could lead to the absence of a response.

We cannot be certain that vibrations, which wall contact might set up in the intact flagellum and might be transmitted to the base, would be equally transmitted in the cut-and-paste situation. The glue and the manipulated distal end of the flagellum might partially filter out any such vibrations. However, the total absence of any response in the cut-and-paste trials and the fully normal responses of the trials with a glued antenna suggest that by far the most significant input for this behavior is from the flagellum.

In summary, these experiments offer strong support for the antennal flagellum being by far the dominant source of sensory input controlling the turning responses to wall projections. We will consider in the Discussion the problem that the long neural conduction distance along the flagellum, in axons of small diameter, appears to be inconsistent with a short-latency behavioral response.

How does the cockroach execute its turns in relation to the wall? This does not occur as a rotation of the body about a set of six legs that simply continue to run straight; rather, the legs must somehow alter their stepping pattern to produce the turns. This is clear, for instance, from Fig. 3A, which shows that the total lateral displacement of the body in the sequence of turns is greater than could be accounted for if the legs maintained a straight, unaltered run.

One possible change of stepping pattern would be a switch

to a different form of inter-leg coordination during a turn as opposed to a straight run. This is known to occur, for instance, when a slowly walking cockroach is presented with an escape-inducing wind stimulus, from which it turns away (Camhi and Levi, 1988). That is, whereas walking involves the well known tripod inter-leg coordination, in which three legs are in the stance phase while the other three are in the swing phase (each leg in phase opposition to its contralateral homolog), the escape turn begins with either five, or all six, legs

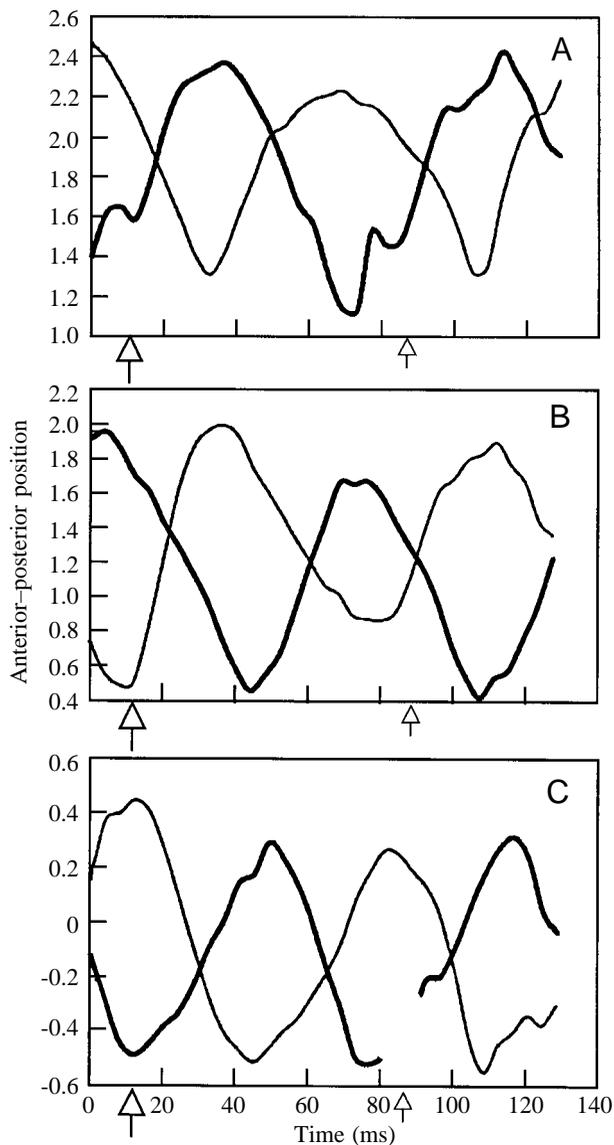


Fig. 9. The anterior-posterior positions of each of the cockroach's six legs during an outward turn in response to an outward wall projection. Same trial as in Figs 7 and 8. (A) Front legs. (B) Middle legs. (C) Hind legs. On each graph, the bold line represents the leg close to the wall, and the thin line represents the opposite leg. The first arrow represents the time of onset of antennal contact, and the second arrow represents the time of loss of antennal contact. For a brief interval, the wall-side hind leg was hidden by the body. Ordinate scale, anterior-posterior position along the body; upward represents more anterior. A value of 1 represents the level of the rear end of the body, and a value of 2 represents the level of the head.

simultaneously coming into stance phase and pushing off against the ground (Camhi and Levy, 1988). Does such a switch occur in the turns induced in running cockroaches by contact with a wall projection?

Fig. 9 shows the running cycle for all six legs during the same trial as in Figs 7 and 8. It is clear that the tripod inter-leg coordination remained intact during the turn, each leg continuing in opposite phase to its contralateral homolog. There was no gross distortion of the inter-leg timing, such as five or all six legs stepping together, as described above for the wind-evoked escape turns of slowly walking cockroaches.

In examining the timing of a given leg relative to its contralateral homolog in 11 runs for five different cockroaches past a single outward wall projection, we obtained the phases shown in Table 2. We calculated the phase of the leg away from the wall within the step cycle of the leg towards the wall. We subdivided the data into three types of sample, as follows: (1) the step just before the antenna touched the wall projection; (2) the mean of all steps (usually just one) during wall contact; and (3) the step just after contact had ended. All phases remained very close to 0.5, indicating a continuation of alternating rhythms of contralaterally homologous legs. There were no significant differences among the different legs or among the three different intervals ($P=0.58$ and 0.62 , respectively; Kruskal-Wallis test). These results are consistent with stepping patterns of cockroaches of a different species (*Blaberus discoidalis*) executing turns while walking on a treadmill (Watson and Ritzmann, 1998).

Given that the basic timing of the stepping pattern is maintained during the turn, the turn would seem to be executed by changes in the direction of stepping during the ongoing rhythm. Such directional changes were beyond the scope of this study.

Discussion

In this paper, we have presented evidence that cockroaches use their antennae both to orient to a straight wall and to respond to wall projections. The evidence regarding the straight wall is that the cockroach contacts the wall with its ipsilateral antenna, and the more of the antennae we removed, the closer the cockroach walked to the wall (Fig. 2). The evidence with regard

Table 2. Phase of a given leg (front, middle or hind) on the side away from the wall with respect to the cycle of the opposite leg

Legs	Before	During	After
Front	0.5±0	0.53±0.08	0.52±0.10
Middle	0.48±0.16	0.56±0.14	0.48±0.13
Hind	0.54±0.07	0.52±0.10	0.46±0.10

Phase (mean ± s.d., $N=11$ runs for five cockroaches) is shown at moments before antennal contact with the wall projection, during antennal contact and after contact has been lost.

As a measure of cycle time for these calculations, we selected a cycle that was completed before any leg contacted the wall.

to wall projections was as follows: (1) projections that were not contacted by the antenna almost never evoked outward turns (only 7%), whereas those that were contacted evoked outward turns on over 60% of the trials; (2) cockroaches with their eyes and cerci removed negotiated multiple wall projections in a normal manner; (3) in our 'cut-and-paste' experiments, where the antennal flagellum ipsilateral to the wall had been deafferented, the cockroaches never responded to a wall projection; yet the opposite intact antenna continued to mediate normal responses; and (4) the flagellar bend and contact point each vary systematically in a way that could provide reliable information regarding outward and inward wall projections.

There remains the enigma of how sensory fibers, presumably of small diameter and thus slow spike conduction velocity, excited far out on the antennal flagellum, can evoke a short-latency turn. The mean turn latency of intact cockroaches was 29 ms, and for the control antenna of the experimental cockroaches (Table 1) the mean latency was 31–32 ms. If one assumes that the antennal cue giving rise to the onset of the behavior occurs 3 cm distal from the antennal base (probably an underestimate), a conduction velocity of 1 m s^{-1} would occupy the full behavioral latency, simply for getting the first spike to the brain. If the conduction velocity were 1.5 m s^{-1} , this would occupy 20 ms, leaving 10 ms for the activation of central circuitry and the start of the behavior. This 1.5 m s^{-1} conduction speed, then, would appear to be the bare minimum that could possibly account for the behavioral latency.

The conduction speed of the flagellar mechanoreceptive axons is not known. For comparison, however, the highest conduction rate of the cercal mechanoreceptive afferents appears to be approximately 3.5 m s^{-1} (Hammon et al., 1990). One might expect the axon diameters, and hence the conduction speeds, of the antennal mechanoreceptor axons to be slower than those of the cerci, given that the antennal nerve, although of modest diameter, contains a very large number of axons (Seelinger and Tobin, 1982). However, there are some hints that spike conduction in antennal mechanoreceptors may nevertheless be relatively rapid. The three types of mechanoreceptor in the flagellum (those of the chemo-mechanoreceptor hairs, the campaniform and the marginal sensilla) all have dendrites of greater diameter than any of the flagellar chemoreceptors (Toh, 1977). In fact, recordings over the mixed chemo-mechanoreceptive hairs show that the spikes of the mechanoreceptor cell, which is strictly phasically active, are consistently larger than those of the chemoreceptors from the same hair (Rüth, 1976). It is possible, then, that the mechanoreceptor's axon is likewise thicker than those of the chemoreceptors.

Touching an antenna of a stationary cockroach, especially with a highly textured object, often induces an escape turn (Comer et al., 1994). The latency from touch to behavioral onset is approximately 25 ms, very close to the latency we observe. It is not known, however, whether flagellar or basal receptors or both contribute to evoking this escape turn. Interneurons with axons of large diameter (up to $40 \mu\text{m}$) and rapid spike conduction velocity (3 m s^{-1}), excited by unidentified antennal

mechanoreceptors, are known to descend from the brain through the thoracic ganglia (Burdohan and Comer, 1990). Metathoracic interneurons known to evoke escape behavior are excited with an excitatory postsynaptic potential in as little as 5 ms following mechanical stimulation of the antennae, the specific mechanoreceptive source again being unknown (Ritzmann and Pollack, 1994). Interestingly, these neurons followed, with only partial decrement, repeated mechanical stimulation of an antenna, even at stimulus frequencies above 50 s^{-1} . Thus, at least some antennal mechanoreceptors and at least some thoracic neurons are able to follow antennal mechanical stimulation at frequencies even higher than the maximal rate at which we have found cockroaches to follow wall projections, 25 s^{-1} .

One possible explanation for these rapid responses would be that the cockroach normally runs in a zigzag pattern and that the antennal contact with the wall merely synchronizes the next zigzag. This does not appear to be the case, however. With a mean outward turn size in response to wall contact of 25° , we would surely have noted such turning in a cockroach running along a straight wall or out in the open of the arena if it had occurred. Although we did not study this question in detail, the largest zigzags we generally could measure on such turns were of less than a few degrees and were of irregular timing.

One way of thinking of the cockroach's turning response away from an outward wall projection is as an obstacle-avoidance mechanism. Other rapidly locomoting animals also have obstacle-avoidance mechanisms. For instance, flying locusts produce steering avoidance responses to visual stimuli simulating the approach of the insect to an obstacle (Robertson and Johnson, 1993; Hatsopoulos et al., 1995). Also, the nucleus rotundus of the pigeon has neurons selectively responsive to visual stimuli simulating direct approach (Wang and Frost, 1992).

Nocturnally active animals, of course, are required to use non-visual cues for such obstacle avoidance. Bats are extremely skilled at doing so using echolocation. Aside from the work we present here on cockroaches, we are unaware of other studies on the use of tactile cues specifically for obstacle avoidance in locomotion, although many species, ourselves included, are probably capable of this. Indeed, tactile cues are able to provide various animals with detailed information. For instance, blindfolded rats are able to use their vibrissae to make fine tactile discriminations (Carvel and Simons, 1990). Human subjects can discriminate the location of a tactile stimulus applied to the finger pad with an accuracy greater than $400 \mu\text{m}$ (Wheat et al., 1995).

The cockroach is able to change its body orientation very rapidly, up to 25 times s^{-1} , in response to sensory cues (Fig. 4B). We know of no other orientation behavior in any animal capable of such a high frequency of body turning. In fact, one insect (*Fannia canicularis*) well known for its acrobatic orientation skills (a fly that chases other flies) operates in a considerably lower dynamic range. Examining published records, it appears that, although the turning angles can be very large, their frequency is well under 10 s^{-1} (Land and Collett, 1974). Moreover, in experimental tests, this turning behavior was shown to follow visual stimuli oscillating at frequencies only up to approximately 5 Hz (Egelhaaf, 1987).

If the cockroach uses the position of the antennal bend point and/or the contact point to initiate a turn, one can think of the antenna as having a one-dimensional sensory map along its flagellum. The location along this map of excited sensory cells would provide the sensory information. A similar map has been discovered in the antenna of the crayfish *Cherax destructor* (Zeil et al., 1985). The movement of a bend, or a wave, along a one-dimensional map recalls the situation in the mammalian cochlea. For instance, in a frequency-modulated bat, the frequency-modulated cry or echo causes a rapid sweep of displacement along the basillar membrane, not unlike that seen in the cockroach antennae (e.g. Suga, 1994).

By holding its antenna at a reasonably fixed angle as it negotiates a wall with or without projections, the cockroach obtains, apparently from the position of antennal contact or bend, a measure of distance from the wall. It thus registers, as a function of time, the one-dimensional scalar parameter of wall position and uses this to control, also as a function of time, a one-dimensional output parameter, turning angle.

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References

- Ahl, A. S.** (1986). The role of vibrissae in behavior: a status review. *Vet. Res. Commun.* **10**, 245–268.
- Bittner, G. D.** (1988). Long-term survival of severed distal axonal stumps in vertebrates and invertebrates. *Am. Zool.* **28**, 1165–1179.
- Burdohan, J. A. and Comer, C. M.** (1990). An antennal-derived mechanosensory pathway in the cockroach: Descending interneurons as a substrate for evasive behavior. *Brain Res.* **535**, 347–352.
- Camhi, J. M. and Levy, A.** (1988). Organization of a complex movement: Fixed and variable components of the cockroach escape behavior. *J. Comp. Physiol.* **163**, 317–328.
- Camhi, J. M. and Macagno, E.** (1991). Using fluorescence photoablation to study the regeneration of singly cut leech axons. *J. Neurobiol.* **22**, 116–129.
- Camhi, J. M., Tom, W. and Volman, S.** (1978). The escape behavior of the cockroach *Periplaneta americana*. II. Detection of natural predators by air displacement. *J. Comp. Physiol.* **128**, 203–212.
- Campbell, F. L.** (1972). A new antennal sensillum of *Blattella germanica* (Dictyoptera: Blattellidae) and its presence in other Blattaria. *Ann. Ent. Soc. Am.* **65**, 888–892.
- Carvel, G. E. and Simmons, D. J.** (1990). Biometric analyses of vibrissal tactile discrimination in the rat. *J. Neurosci.* **10**, 2638–2648.
- Comer, C. M., Mara, E., Murphy, K. A., Getman, M. and Mungy, M. C.** (1994). Multisensory control of escape in the cockroach *Periplaneta americana*. II. Patterns of touch-evoked behavior. *J. Comp. Physiol.* **174**, 13–26.
- Delcomyn, F.** (1971). The locomotion of the cockroach *Periplaneta americana*. *J. Exp. Biol.* **54**, 443–452.
- Dreller, C. and Kirchner, W. H.** (1993). How honeybees perceive the information of the dance language. *Naturwissenschaften* **80**, 319–321.
- Egglehaaf, M.** (1987). Dynamic properties of two control systems underlying visually guided turning in house flies. *J. Comp. Physiol.* **161**, 777–783.
- Gras, H., Hörner, M. and Schürmann, F.-W.** (1994). A comparison of spontaneous and wind-evoked running modes in crickets and cockroaches. *J. Insect Physiol.* **40**, 373–384.
- Guthrie, D. M. and Tindall, A. R.** (1968). *The Biology of the Cockroach*. London: Edward Arnold Ltd.
- Hammon, A., Guillet, J. C. and Callec, J. J.** (1990). A gradient of synaptic efficacy and its presynaptic basis in the cercal system of the cockroach. *J. Comp. Physiol.* **167**, 363–376.
- Hatsopolous, N., Gabbiani, F. and Laurent, G.** (1995). Elementary computation of object approach by a wide-field visual neuron. *Science* **270**, 1000–1003.
- Kirchner, W. H.** (1994). Hearing in honeybees: The mechanical response of the bee's antenna to near field sound. *J. Comp. Physiol.* **175**, 261–265.
- Land, M. F. and Collett, T. S.** (1974). Chasing behavior of houseflies (*Fannia canicularis*). *J. Comp. Physiol.* **89**, 331–357.
- Pass, G.** (1985). Gross and fine structure of the antennal circulatory organ in cockroaches (Blattodea, Insecta). *J. Morph.* **185**, 255–268.
- Ritzmann, R. E. and Pollack, A. J.** (1994). Response of the thoracic interneurons to tactile stimulation in the cockroach, *Periplaneta americana*. *J. Neurobiol.* **25**, 1113–1128.
- Ritzmann, R. E., Pollack, A. J., Hudson, S. E. and Hyvonen, A.** (1991). Convergence of multi-modal sensory signals at thoracic interneurons of the escape system of the cockroach, *Periplaneta americana*. *Brain Res.* **563**, 175–183.
- Robertson, R. M. and Johnson, A. G.** (1993). Collision avoidance of flying locusts: steering torques and behavior. *J. Exp. Biol.* **183**, 35–60.
- Rüth, E.** (1976). Elektrophysiologie der Sensilla Chaetica auf den Antennen von *Periplaneta americana*. *J. Comp. Physiol.* **105**, 55–64.
- Schaller, D.** (1978). Antennal sensory system of *Periplaneta americana* L. *Cell Tissue Res.* **191**, 121–139.
- Schmidt, K.** (1969). Die campaniformen Sensillen im Pedicellus der Florfliege (*Chrysopa*, Planipennia). *Z. Zellforsch.* **96**, 478–489.
- Seelinger, G. and Tobin, T. R.** (1982). Sense organs. In *The American Cockroach* (ed. W. J. Bell and K. G. Adiyodi), pp. 217–245. London: Chapman & Hall.
- Shafer, R. and Sanchez, T. V.** (1973). Antennal sensory system of the cockroach *Periplaneta americana*, postembryonic development and morphology of the sense organs. *J. Comp. Neurol.* **149**, 335–354.
- Suga, N.** (1994). Multi-function theory for cortical processing of auditory information: Implications of single-unit and lesion data for future research. *J. Comp. Physiol.* **175**, 135–144.
- Toh, Y.** (1977). Fine structure of antennal sense organs of the male cockroach, *Periplaneta americana*. *J. Ultrastruct. Res.* **60**, 373–394.
- Wang, Y. and Frost, B. J.** (1992). Time to collision is signaled by neurons in the nucleus rotundus of pigeons. *Nature* **356**, 236–238.
- Watson, J. T. and Ritzmann, R. E.** (1998). Leg kinematics and muscle activity during treadmill running in the cockroach, *Blaberus discoidalis*. I. Slow running. *J. Comp. Physiol.* **182**, 11–22.
- Wheat, H. E., Goodwin, A. W. and Browning, A. S.** (1995). Tactile resolution: Peripheral neural mechanisms underlying the human capacity to determine positions of objects contacting the fingerpad. *J. Neurosci.* **15**, 5582–5595.
- Zeil, J., Sandeman, R. and Sandeman, D.** (1985). Tactile localization: The function of active antennal movements in the crayfish *Cherax destructor*. *J. Comp. Physiol.* **157**, 607–617.