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PATTERNS OF TURNING IN COURTSHIP ORIENTATION OF THE MALE GERMAN COCKROACH

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Abstract. Courtship turning of the male German cockroach, *Blattella germanica*, was analysed with respect to rotational and translational movements. Three different sources of orientation information are postulated for the control of this behaviour: external sensory information (perception of sex pheromone) releases courtship, proprioception from the legs is required to curtail turning when the specified turn angle is reached, and internally stored information determines the sign of turning and patterns the courtship actions.

Courtship of the male German cockroach, *Blattella germanica*, consists of a sequence of acts initiated by perception of female sex pheromone (Roth & Willis 1952; Bell et al. 1978b). Two strategic turns are executed by the male during courtship. The first turn of approximately 180° orients the abdomen toward a female in a precopulatory position to facilitate and elicit mounting by the female; the second turn of approximately the same dimension orients the head back to its original position if the female does not mount the male's abdomen.

Courtship turning lends itself to experimental analysis because the sex pheromone stimulus can be quite accurately controlled and the resulting turns easily measured. Subject to the limitations of ethometric analysis, the present paper attempts to characterize the relative roles of different types of orientation information and to analyse the patterning of male courtship movements in terms of an adaptive strategy for maintaining close contact between courtship partners.

Methods

Adult male *Blattella* were removed from colonies and isolated from females for two to nine days. We continually maintained, replacing groups as needed, five cages of 50 isolated males, kept at 26 C and 60% R.H. in a 12h light: 12h dark regime. All tests were performed on individual cockroaches 2 to 4 h after the onset of the scotophase, under simulated dark conditions with 60-W G.E. Ruby lamps (595–650 nm).

Synthetic sex pheromone, a 50:50 mixture of 3, 11-dimethyl-2-nonacosanone and 29-hydroxy-3, 11-dimethyl-2-nonacosanone, was employed at a concentration of 100 µg/ml in carbon tetrachloride unless otherwise stated (Burgstahler et al. 1975, 1977; Bell et al. 1978a, 1978b).

Previous studies have shown that courtship behaviour in the German cockroach includes antennation of the female by the male, presumably allowing the latter to perceive sex pheromone on the cuticular surface of the female (Roth & Willis 1952). Methods employed here are described in detail by Bell et al. (1978a), where antennae used were ablated from male *Periplaneta americana* to eliminate any possible non-chemical stimuli specific to German cockroaches. Freshly ablated antennae fixed to 20-cm glass rods were dipped into a pheromone/carbon tetrachloride solution for 1 to 2 s; these were then allowed to dry for 30 s prior to use. The manipulated antenna was then touched to one or both antennae of a male cockroach in a test cage for 1 to 2 s. Responses were recorded as follows.

Bell (1978) described a technique for measuring turning angles of cockroaches in the context of agonistic behaviour. This method was employed in the present study, where a turntable was positioned beneath a cage holding a male cockroach. The surface of the turntable was drawn with parallel lines (4 mm apart) and compass readings 0° to 360° at the perimeter. The dimension of any turn executed by a cockroach could be ascertained by recording the original position of the animal and the position after a turn was executed. The angle of the turn was calculated by subtracting the two values. In experiments presented in this paper a male cockroach was stimulated by contact with a pheromone source, the stimulus was removed, and then the resulting turning angle was recorded. Each cockroach was tested only once in a given experimental series.

Circular distributions of turning-angle data were treated statistically according to Batschelet (1965). The data from each experiment were first subjected to the Rayleigh statistic to determine whether the distributions were unimodal, i.e. was there a single preferred direction? All distributions of cockroach-turning data were found to have preferred directions ($Z \geqq 109$, $P < 0.0001$). The distributions were skewed rather than normally distributed (see Fig. 1), and so the mode and range are used to indicate the central tendency and variation. Because the data were not normally distributed, a non-parametric test, the modified χ^2 of Batschelet (1965), was used to test for significant differences among turn angle distributions.

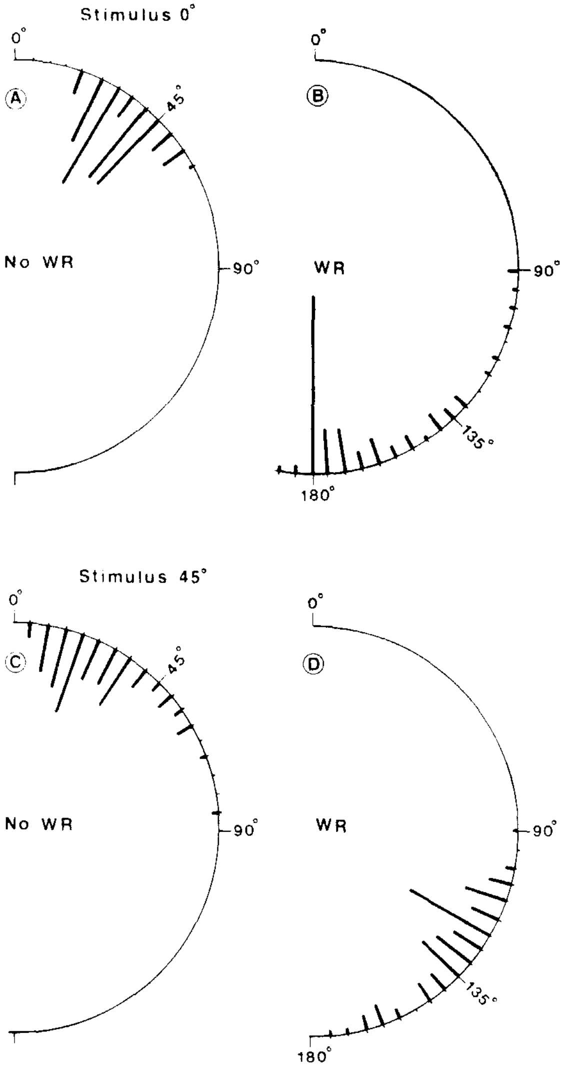

Fig. 1. Diagrammatic representation of distributions of T_1 turn angles of intact males resulting from a stimulus at 0° or 45°. WR, Courtship actions such as Wing Raising and Abdominal Extension.

Turns of male cockroaches were recorded at 24 frames/s or faster using a Baillieau super-8 camera. Films were projected onto a protractor table with a Lafayette film analyser. Body and head movements, walking patterns of legs, and sweeping movements of antennae were quantified by measuring angular deviations of the body, legs, and antennae in successive frames of film.

Results

Description of Courtship Orientation

Males exhibited courtship actions such as Alert Posture followed by Wing Raising and Abdominal Extension during the first phase of courtship orientation, referred to as a type one turn (T_1). This manoeuvre terminated with the abdomen oriented toward the stimulus (test antenna). A stationary posture with wings raised was maintained if the test antenna was manipulated to probe the tergal gland on the dorsal part of the abdomen, thus simulating the mounting actions of a female. In the absence of such stimuli to the abdomen, the male lowered its wings and executed a second turn (T_2) back to approximately its original position. In addition to these rotational movements about a central pivot point, translational movements consisted of backing movements during T_1 turns and forward movements during T_2 turns.

Rotational Movements in T_1 Turns

In the first experimental series equal stimulation was applied to each antenna of 200 intact males to duplicate the conditions of a female exactly in front of the male, i.e. 0° with respect to the longitudinal body axis. As shown in Table I and Figs. 1A and B, a stimulus at 0° resulted in two classes of T_1 turns. First, 10% of 200 tests resulted in relatively small turns (mode = 30°) performed without courtship actions. Second, the majority of turns (90%) were approximately 180° and occurred in conjunction with male courtship actions, such as Wing Raising and Abdominal Extension. Approximately equal numbers of left and right turns were recorded for both classes of turns, and so the direction of turn was disregarded in analysing the data in this series of experiments.

In a second series of experiments, either the right or left antenna was stimulated as it was deflected and held outward by the male. This procedure duplicated the conditions of a female

Table I. Dimensions of Rotational Turning in Type One Turns (T_1)*

	Direction of stimulus			
	0° (− courtship)	0° (+ courtship)	45° (− courtship)	45° (+ courtship)
Intact	30° (20°–60°)	180° (90°–190°)	20° (5°– 85°)	120° (90°–175°)
−prothoracic leg	50° (15–65°)	180° (135°–220°)	30° (10°–105°)	160° (95°–205°)
−mesothoracic leg	40° (10°–65°)	180° (130°–225°)	40° (15°– 85°)	155° (85°–190°)
−metathoracic leg	35° (10°–75°)	180° (140°–215°)	40°(5°– 90°)	165° (95°–185°)
−antenna			45° (15°–100°)	135° (100°–180°)

*$N = 200$ males for each experimental type tested at 0° and 200 males for each experimental type tested at 45°; turning dimensions are given as mode and range (parentheses).

positioned approximately 45° to the longitudinal body axis. Two classes of T_1 turns were recorded (Table I and Figs. 1C and D). First, 58% of 200 tests resulted in relatively small turns (mode = 20°) without courtship actions, but with the head invariably orienting toward the direction of the stimulated antenna (left or right). Second, 42% of the tests resulted in larger turns (mode = 120°) with the head orienting away from the direction of the stimulus and in conjuction with courtship actions. These latter turns resulted in the positioning of the abdominal tip near to the location at which antennal stimulation occurred. In other words, a stimulus at ca. 45° to the right led to a ca. 135° turn with the head orienting toward the left. This is opposed to a possible alternative response giving the same end result, a turn of 225° to the right. Courtship turns resulting from a stimulus at 45° are significantly different from those resulting from a stimulus at 0° ($P < 0.001$; modified χ^2). There is evidence, therefore, for modulation of the dimensions of T_1 turning angles depending on the direction of the stimulus source.

A threshold effect, whereby small turns without courtship result from insufficient sensory information, initially seemed to explain the two classes of turns found in experiments 1 and 2. The possibility that the differential was due to concentration of pheromone was tested in a third series of experiments in which samples of different pheromone concentrations were used. A serial dilution of 100 mg/ml to 0.01 μg/ml was tested; it was found that no responses were elicited with less than 1 μg/ml and avoidance by males always occurred when concentrations higher than 10 mg/ml were tested. Within the effective range of concentrations, i.e. 1 μg to 10 mg, the ratio of small to large turns was constant (χ^2), suggesting that the threshold for large turns with courtship behaviour applies to tactile sensory input and not to chemical sensory input.

If the angle of a courtship turn is determined by a specific number of leg movements programmed by a 'turn generator', then removal of one or more legs should result in a turn that is smaller than those observed in intact males. On the other hand, if turn dimensions are controlled through feedback from proprioceptors in the legs, then the removal of one or more legs might result in various degrees of 'overshooting'. Tests were performed as described above using males three days after the ablation of one prothoracic, mesothoracic, or metathoracic leg. As shown in Table I, the turns fell into two classes similar to those exhibited by intact males. Stimulation of both antennae (0°) resulted mainly in 180° turns associated with courtship actions. Of those turns that were not 180°, however, more than 50% were larger than 180° as compared to less than 5% of turns larger than 180° in intact males. The two distributions are significantly different ($P < 0.001$; χ^2) owing to a shift in the values from less than 180° to greater than 180°. This tendency is referred to here as 'overshooting'. No significant differences were found among distributions resulting from tests of males with one prothoracic, mesothoracic, or metathoracic leg excised. Smaller turns without courtship actions also occurred as in intact males. Unilateral antennal stimulation (45°) resulted in two classes of turns. Those that were associated with courtship actions (60%) had distributions significantly different from those of intact males for homologous types of turns ($P < 0.001$; χ^2). No significant differences were found among distributions resulting from tests of males with one prothoracic, mesothoracic, or metathoracic leg excised. Smaller turns without courtship actions also occurred as in intact males (40%).

Apparently the dimensions of T_1 turning angles are controlled by feedback rather than by the execution of programmed stepping patterns. Turning continues past the normal stopping point in the absence of the total quantity of feedback information.

Results of stimulating one of the antennae of intact males suggested that input from the antennae is involved in specifying the position of the stimulus. Therefore, a male with only one antenna would be expected to perform as though only one antenna was stimulated. This prediction was not borne out by experimentation. Two classes of turns resulted when the remaining intact antenna was stimulated (Table I). About half of 200 turns recorded (57%) were relatively small (mode = 45°), and were not associated with courtship actions. In contrast to small unit turns in intact animals, unilaterally antennectomized males turned their head away from the stimulated intact antenna in all cases. Turns that were larger (mode = 135°) and associated with courtship actions (43%) were not significantly different from those of intact males stimulated at 45°. The small turns directed away from the stimulus suggest that unilateral antennectomy interferes with the ability of a male to specify from antennal input the position of a stimulus source. On the other hand, turns associated with courtship actions are carried out as in intact males.

Rotational Movements in T_2 Turns

T_1 turns were followed by T_2 turns in 83% of tests with intact males; in 17% the males remained stationary for several seconds and then wandered away. Data from all $T_1 - T_2$ sequences recorded (at 0° stimulus) show that the T_2 turn is not necessarily a true 'counterturn' as described in the orientation literature. Frequencies of the four possible directional combinations of $T_1 - T_2$ sequences were as follows: left-left, 0; right-right, 17.3%; left-right, 17.3%; and right-left, 65.4%. Thus in 82.7% the T_2 turn was in the opposite direction from the T_1 turn, and in 17.3% they were in the same direction.

There was no significant difference between T_2 turns of males stimulated at 0° compared to those stimulated at 45°; both have a mode of 180° and a distribution of 90° to 185°. A correlation analysis was performed between the T_1 and T_2 turns of each sequence to determine whether large T_1 turns were followed by large T_2 turns and small T_1 turns followed by small T_2 turns. There was no correlation ($r = 0{\cdot}23$), however, suggesting that the dimensions of T_2 turning angles are independent of T_1 turns, rather than controlled by a mechanism that simply repeats in reverse the locomotory movements and consequently the angular dimensions of a T_1 turn.

T_2 turns of males with one leg ablated were significantly larger (for 0° stimulus, mode = 180°, range = 140° to 220°; for 45° stimulus, mode = 180°, range = 135° to 225°) than those of intact males ($P < 0.001$; χ^2), indicating that proprioception is required for T_2 turning. T_2 turns of cockroaches with one antenna were not significantly different ($P > 0.10$; χ^2) from those of intact males.

A clue to the control of the dimensions of T_2 turn angles was obtained by reviewing films of the courtship behaviour of males interacting with actual females. T_2 turns of males courting females seldom exceeded 160°, although quantification was difficult because the turntable apparatus could not be 'pre-set' in experiments with moving males and females. Detailed analysis of the films suggested that the turning movements of a male were arrested when one of the antennae contacted a female. This was tested by touching the leading antenna (toward the turn direction) of a male with the test antenna during a T_2 turn. In all cases ($N = 100$) the male stopped turning even when the test antenna was not impregnated with sex pheromone. Interestingly, this mechanism of modulating the dimension of a T_2 turn angle does not apply to T_1 turns. Touching the antenna of 50 males engaged in the first turn did not curtail movement once it had been initiated.

Translational Movements in T_1 and T_2 Turns

In addition to rotational movements of predictable angular dimensions, courtship orientation is also characterized by lateral and axial displacement of the body. Such movements are referred to as translation. Frame-by-frame film analysis of 12 $T_1 - T_2$ turn sequences of intact males generated measurements for these movements.

No differences were observed in the characteristics of $T_1 - T_2$ sequences that were in the same direction (e.g. right-right) compared to those in opposite directions (e.g. left-right). Both types of turns are therefore pooled in the following analysis. In the discussion below, the term 'direction of turn' refers to the direction (left or right) of movement by the head, and 'leading' or 'following' antennae refer to antennal alignment with respect to the direction of turn. Thus during a right turn the right antenna is the leading antenna.

Both T_1 and T_2 turns are characterized by lateral and axial translation as illustrated in the drawings traced from photographic films (Fig. 2) and as graphed in Fig. 3. Lateral translation occurs in 88% of T_1 turns, and in all cases the displacement is in the direction of turn (mean = 4.8 mm, range 0 to 9.2 mm). Lateral translation occurs in 80% of T_2 turns, only 60% in the direction of turn, and to a lesser extent than in T_1 turns (mean = 2.2 mm, range 0 to 4.2). Most T_1 turns entail axial movement backwards (mean = 2.9 mm, range 0 to 5.5 mm), whereas T_2 turns entail axial movement forward (mean = 2.9 mm, range 0 to 9.7 mm).

Forward or backward movement during turning can be accomplished in only three ways: by alterations in the position of the pivot point, by forward or backward stepping, or by a combination of both. The influence of pivot position was analysed by comparing mean pivot positions (length from head to pivot) for each T_1 and T_2 turn. The mean pivot point for T_1 turns was significantly less than that for T_2 turns ($P <$ 0.001) in 83% of turns analysed. Figure 3 illustrates the influence of the pivot point on forward or backward translation. The reference line indicates translation that would result from a change in the pivot point of the body from the centre of the longitudinal axis of the body. In other words, if the pivot point is very close to the head, then a turn will result in backward displacement of the body. Most T_1 turns result in translation backwards, and since most data points for T_1 turns in Fig. 3 are above the reference line, the displacement of the body is due to backward walking as well as a forward positioning of the pivot point. A similar situation pertains to T_2 turns, except that forward translation results owing to forward walking and backward positioning of the pivot point.

More time is required to complete T_1 turns (mean = 1.54, range 0.83 to 2.50 s) than T_2 turns (mean = 0.78, range 0.46 to 1.54 s). This means that turning occurs at a rate of 1.868 radians per s for T_1 and 4.259 radians per s for T_2 turns. In order to graph the rate of turning, the time base was converted from seconds to percentage of completion time. For example, the value 50% represents the quantity of turn completed at 1.2 s in a turn that required a total of 2.4 s. The curves generated for angular movement of the body versus completion time (Figs. 4 and 5) are different mainly in that the lag phase noted in the T_1 curve is absent in the T_2 curve; this difference reflects the faster rate of movement in T_2 turns.

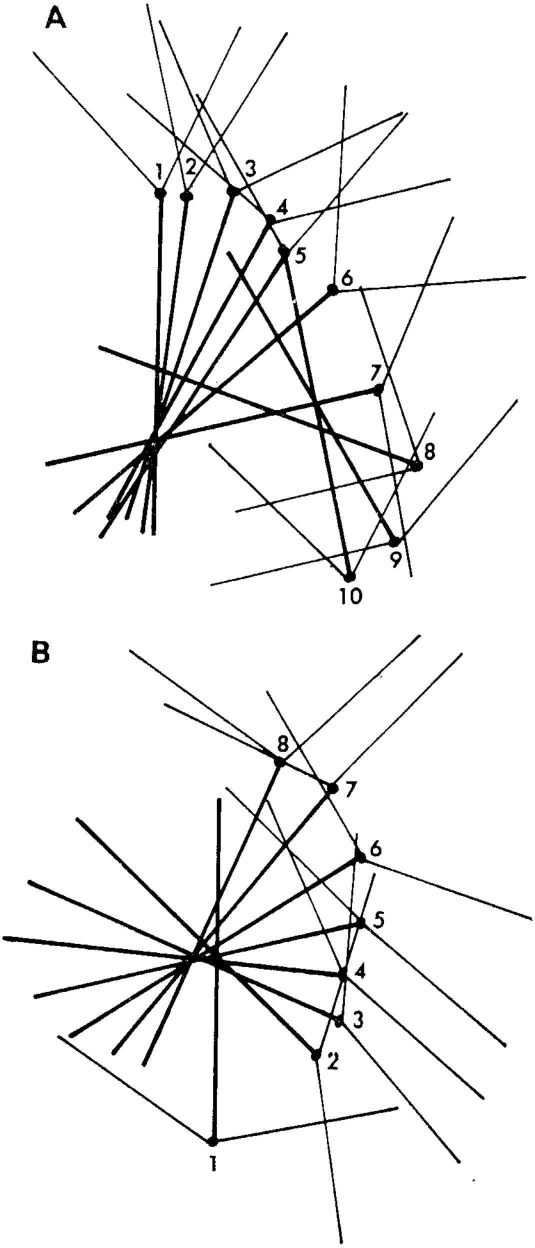

Fig. 2. Body and antennal movement patterns of an intact male during a T_1 turn (A) and a T_2 turn (B). Numbers indicate relative sequence of movement. Solid dots show position of the head. In all cases the stimulus is directly in front of the male.

Antennal Movements

Individual antennae move independently of each other, i.e. sweeping movements of different antenna are not correlated positively or negatively with each other. If the overall patterns are considered, however, there are distinct movements of the leading and following antennae during the progression of T_1 and T_2 turns (Fig. 2A, B). These movements are depicted and correlated with body turning angles for a typical $T_1 - T_2$ sequence in Figs. 4 and 5. During the beginning of T_1 turns the leading antenna (right antenna in Fig. 4) remained oriented toward the position of the stimulus, which for the first half of the turn resulted in relatively small turning angles. In 75% of T_1 turns the leading antenna crossed over the midline (longitudinal body axis) of its domain, and these angular deviations are represented in Fig. 4 as negative values. In the second half of a T_1 turn the leading antenna deflected posteriorly, again toward the stimulus. The following antenna (the left antenna in Fig. 4) maintained a position approximately 90° from the body axis until the second half of the turn, when it deflected posteriorly toward the stimulus. When the T_2 turn began, both antennae were oriented posteriorly. As turning movements proceeded the leading antenna (left antenna in Fig. 5) slowly deflected anteriorly, whereas the following antenna (right antenna in Fig. 5) quickly moved anteriorly and then deflected in a zone from 30° to 50°. In most cases the antennae were oriented anteriorly toward the position of the stimulus when the T_2 turn was completed.

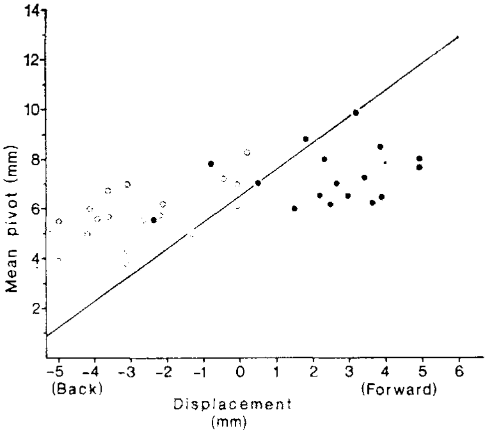

Fig. 3. Axial displacement (abscissa) correlated with mean pivot point (distance from head to pivot point) during T_1 (open circles) and T_2 (closed circles) turns.

Sweeping of antennae was generally characterized by small sequential deflections (less than 50°), although larger deflections up to 180° did occur.

Discussion

Courtship orientation of the German cockroach is controlled by a combination of extrinsic and intrinsic information. The first type of information, extrinsic sensory, is gained from the antennae. Because vaporized sex pheromone

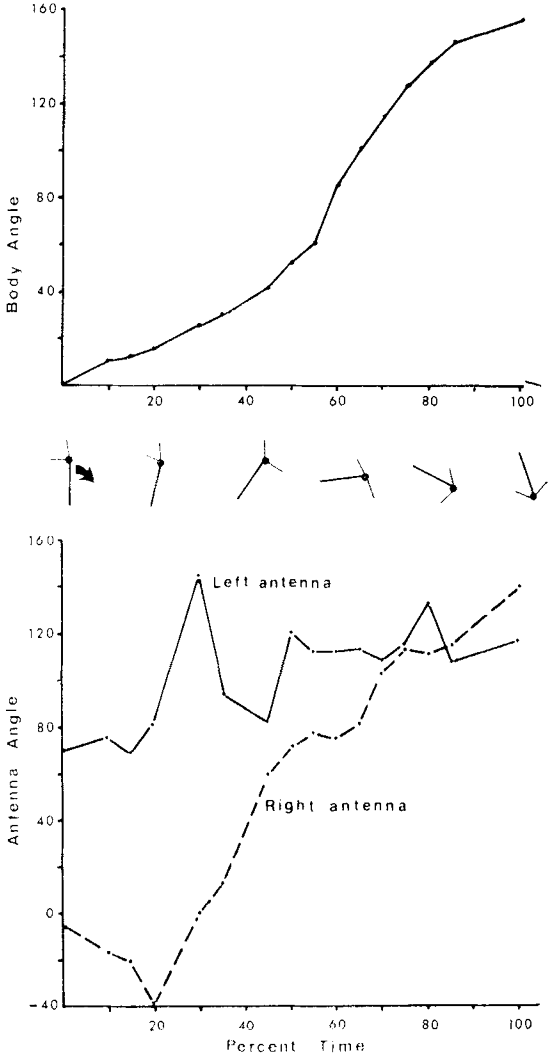

Fig. 4. Body (above) and antennal (below) movements during a typical T_1 turn. Small diagrams illustrate alignment of body, head, and antennae during the turn.

evokes neither behavioural nor electroantennagram responses (Bell et al. MS.), contact chemoreception of the odour molecules seems to be required to effect a response. This information has one primary function: the release of courtship behaviour. As would be expected there is a sex pheromone level below which the male fails to initiate courtship. There also seems to be a threshold for the tactile component of the stimulus, below which small turns toward the stimulus occurred without courtship actions.

A second source of orientational information, intrinsic non-sensory, organizes courtship behaviour by specifying the type of locomotion (turning) and the sign (T_1 or T_2 turn), and coordinates the motor program for the legs, antennae, wings, and abdomen. This results in a complex pattern of movements of the body and appendages that does not require continuous perception of sensory information. Once courtship is initiated, all of the actions involved during a $T_1 - T_2$ sequence can be carried to completion without further external sensory information input. The endogenous 'programme' as defined by Hoyle (1976) seems not appropriate for this organizing or patterning capacity, owing to the considerable variation in the sequence of acts that occur during courtship (Bell et al. 1978b).

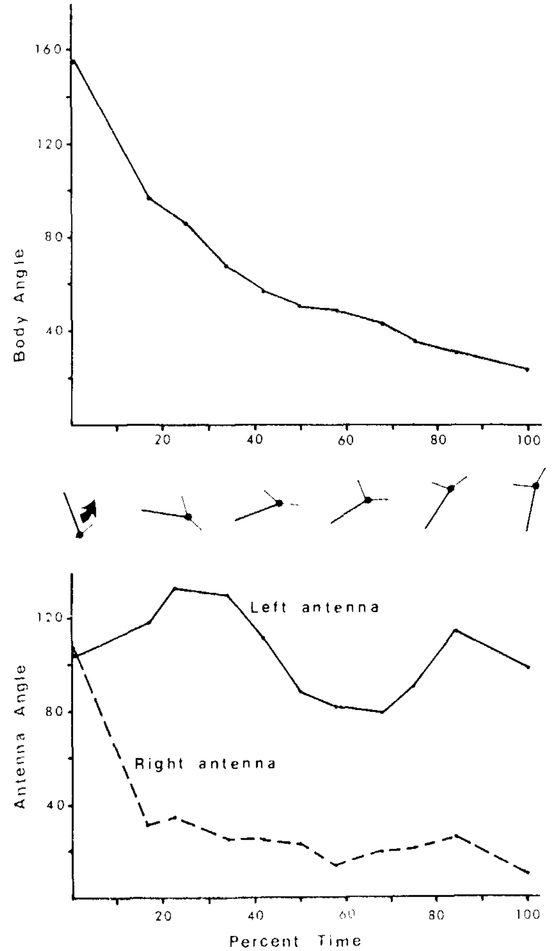

Fig. 5. Body (above) and antennal (below) movements during a typical T_2 turn. Small diagrams illustrate alignment of body, head, and antennae during the turn.

At specific points in courtship orientation it is possible to inject sensory information from antennal or abdominal sensory organs. For example, the T_2 turn does not occur if a female mounts the male or if the experimenter stimulates the dorsal abdomen; instead the male switches to copulatory actions. Contact to the abdomen before the completion of the T_1 turn or after the initiation of the T_2 turn has no effect. A second injection point occurs during the T_2 turn when the leading antenna contacts an object, and this information curtails further turning. The most interesting aspect of intrinsic organizing capacity is the 'comparator' that regulates the turn dimension. Although proprioceptive information from the antennae probably specifies the required turn dimension based on the position of the stimulated antenna, and proprioceptive information from the legs seems to relate progression of turning movements, there must be a mechanism that compares the value of a specified turn with feedback from proprioceptors in the legs.

A third source of information includes two types of proprioception, apparently derived from 'positional sensors' in the antennae and 'movement detectors' in the legs. Reduction in proprioception is indicated by 'overshooting' in the turns of males with one leg ablated. It is interesting that the mode for these turn distributions does not change when one leg is removed, but that the distributions become skewed toward the larger turn angles.

Proprioception as a source of input during locomotion has been investigated in various orthopteran species (e.g. Delcomyn 1971a, 1971b; Pearson & Iles 1973; Pearson et al. 1976; Bassler 1977). Unfortunately, it is not possible to relate this knowledge about feedback in walking to problems that involve turning. For example, ablation of a mesothoracic leg leads to a delay in the protraction of the ipsilateral prothoracic leg in walking (Delcomyn 1971b), but the potential effect of this delay on turning is obscure. In a communication that will follow the present one (Franklin et al. MS) the leg movements involved in cockroach turning are analysed. It is clear from this latter work that the tripod gait common to a walking cockroach (Hughes 1952; Wilson 1966) is greatly modified in turning.

Specification of turn angles, based on feedback from antennal position detectors, seems less than precise, as attested by the relatively large range of turning angles recorded. However, the fact that T_1 turn angles resulting from stimulation at 0° were significantly larger than those resulting from stimulation at 45° suggests that proprioception information from the antennae can be used to specify the dimensions of turns prior to their initiation. The direction of turn is specified as well as the dimensions of turn. Approximately equal numbers of left and right turns were executed when the stimulus was positioned at 0°, but when the stimulus was positioned at 45° the cockroach turned its head away from the stimulus. The abdomen was oriented toward the stimulus, using the shorter 135° turn rather than the alternative 225° turn. The simplest rule to explain this choice is that the cockroach turns away from the antenna that receives the greater quantity of stimulation.

Courtship turning in the male German cockroach is a behavioural adaptation that facilitates copulation by maintaining close contact between sexual partners. Such behaviour in various forms is common among the Blattaria. In *Periplaneta americana* the volatile female sex pheromone provides orientational information (Bell et al. 1977; Hawkins 1978) and releases male courtship (Barth 1970; Simon & Barth 1977). When a male contacts a female it raises and flutters its wings, extends the abdomen, performs T_1 turns, and runs backward toward the female (Barth 1970; Simon & Barth 1977). Unpublished analysis of films showing turns of *Periplaneta* suggests that the dimensions of T_1 turning angles are more variable than those of *B. germanica*, but that chemo-orientation seems to compensate for the inaccurate specification of turn angles. T_2 turns do not occur, although males move quickly about to re-locate the female. In *Nauphoeta cinerea* the male secretes a volatile sex pheromone, seducin, that attracts females and functions as an arrestant (Roth & Dateo 1966). Contact with a female releases Wing Raising and turning movements (Roth & Willis 1954; Roth & Barth 1967), but as with *Periplaneta* the turning angles are variable. Volatile sex pheromones are absent in both sexes of *Blattella* (Roth & Willis 1952; Bell et al. MS), suggesting an enhanced dependence on the accuracy of intrinsically patterned motor actions in courtship orientation. Accuracy derives from the predictable rotational movements that correspond to stimulus position, translation in the direction of the stimulus, independence of T_1 and T_2 turns, and coordination of the antennae during courtship turning. Combined, the accuracy of turn angles and coordination of body and antennal movements compensate for a lack of extrinsic sensory information that guides courtship orientation in many other cockroach species.

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