Sensory Aspects of the Control of Orientation to Prey by the Waterstrider, *Gerris remigis*

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Summary. 1. Sensory aspects of the control of orientation to surface ripples have been examined in the waterstrider. The angular component of the motor response of tethered animals is highly correlated with the angular deviation of a target from the longitudinal body axis (Fig. 1).

2. Amputation of three unilateral legs just proximal to the tibio-tarsal joint blocks normal orientation. Most turns by these preparations are directed toward the intact side irrespective of target position (Fig. 3). Amputations at more distal points on the legs have no observable effect (Fig. 2).

3. Orientation does not depend on a full complement of receptors since responses normally correlated with target deviation do occur when the target is ipsilateral to the intact receptors of a unilaterally amputated preparation (negative target deviations, Fig. 3).

4. A series of ablation experiments suggests that the system may function by determining the receptor nearest the source of ripples since a number of fairly accurate predictions can be made by assuming this is the case (Figs. 5, 6, 7, 9).

5. Each receptor has a negative influence on the torque elicited by an ipsilateral and more posterior receptor.

Introduction

A number of aquatic Hemiptera locate their prey by turning toward disturbances of the water surface. In the genera which have been examined (*Notonecta, Gerris, Velia*) the receptors are associated with the legs but have not been specifically identified (Markl and Wiese, 1969; Rensing, 1960). The receptor mediating orientation to prey by *Notonecta glauca* has been localized in the distal tibia of the pro- and mesothoracic legs (Markl and Wiese, 1969).

The receptors of all three genera have been characterized, through behavioral tests, in terms of their frequency response. The backswimmer (*Notonecta*) responds positively to ripples of 1–2 μ amplitude over a broad range of frequencies (20–150 Hz) (Markl and Wiese, 1969). *Gerris* and *Velia* have similar maximum sensitivities, requiring 4 and 1 μ ripples respectively; however, the frequency band is considerably narrowed with a sharp peak between 150 and 200 Hz (Rensing, 1960). Rensing (1960) also suggests that *Gerris* is responsive to ripples of 20–50 Hz but was

unable to test this in detail. I have confirmed that gerrids do respond to 5 μ ripples at frequencies of 20–30 Hz.

I have shown elsewhere that orientation by *Gerris remigis* consists of a series of discrete turning movements leading to capture of the source of a surface disturbance. The angular component of each motor movement is correlated with the angular deviation of the source of ripples from the specimen's longitudinal body axis (Murphey, 1971).

Analysis of the system controlling orientation to prey would be facilitated if the receptors mediating the response could be precisely localized. Selective ablation of different receptors might then provide some insight into the nature of the interactions between receptor inputs which underlie the localization of a source of surface ripples.

Methods

Wingless females of the waterstrider, *Gerris remigis*, were used throughout these experiments. The specimens were collected in the area surrounding Eugene, Oregon and maintained in the lab in a large tank of running tap water.

Specimens were prepared for testing by attaching a pair of 50 μ silver wires (30–45 cm long) to the prothoracic shield. The tether was then attached to a point directly above the animal, coiled slightly and adjusted so that minimum weight was placed on the preparation. Tethered in this manner, the preparation is confined to a circle approximately 15 cm in diameter. After a movement the animal is swung back to its original body orientation by the tether.

When the effect of amputation of different legs was to be tested, the leg(s) was simply cut off with a fine scissor at the appropriate point, the tether attached and the preparation allowed to recover for 24 hours. Usually the preparations were tested the day following amputation and then discarded. Some experiments demanded that the preparation be tested as long as three consecutive days after the amputation.

A calibrated ripple-producing mechanism was placed 5–7 cm from the tethered animal. This stimulator was constructed by attaching a plastic probe 5 cm long to the diaphragm of a headphone. The stimulator was driven by an audio oscillator (Hewlett-Packard, 202C) The ripples produced were calibrated after the method of Rudolph (1967). Throughout the experiments reported here, the test stimuli were ripples of 20–30 Hz and 10–20 μ in amplitude (measured at the preparation).

The higher frequencies of stimulation (100–200 Hz) were excluded in the analysis because of the difficulty of getting consistent behavioral responses to these frequencies in preparations tethered for long periods of time. The preparations seemed to habituate much more rapidly to these frequencies thereby precluding the necessary number of trials required to estimate the preparation's ability to localize a stimulus.

The changes in body orientation in response to a stimulus were recorded with a closed circuit television system (Bell and Howell). The tether was attached to a mirror placed at an angle of 45° to the water surface, and the TV camera focused on the mirrored image.

A test was conducted in the following manner. The video recording system was turned on, then the stimulator was turned on and the first motor movement which occurred after stimulus onset was recorded. Preparations were tested no more frequently than once every five minutes.

The position of the target with respect to the longitudinal body axis and the post-turn orientation of the body were recorded for analysis by tracing the tape recorded positions on a sheet of acetate placed over the TV monitor. The appropriate measurements (see Fig. 1 in Murphey, 1971, p. 153) were then made and the results plotted as scatter diagrams.

A total of 37 experiments were initiated. The results for 26 preparations are utilized below. The eleven preparations excluded either would not respond at all to artificial stimulation or responded so few times that they provided no information concerning their ability to localize a stimulus. This success ratio is fairly evenly distributed over the entire group of experiments although preparations with only one or two intact legs were less responsive than preparations with less severe ablations.

Results

Localization of a Receptor

Intact, tethered specimens respond to surface ripples with a precise motor response, the nature of which depends on the position of the source of ripples in the space surrounding the animal (Fig. 1). Each turn tends to decrease the angle between the longitudinal body axis and the target. When the target is directly behind the preparation (target deviation = 180°), the motor response is a large turn to either the right or the left. However, even turns which are directed away from the target when the target deviation is large (points in upper left and lower right quadrants of Fig. 1) are adaptive since a large turn in either direction will decrease the angle between the target and the longitudinal body axis. Every possible target position in the space surrounding the animal therefore has a corresponding motor response which tends to aim the animal at the target.

If the receptors are bilaterally situated, and correct orientation depends on the integrity of bilateral groups of receptors, then ablation of a unilateral group of receptors should block normal orientation. Most likely all responses to a stimulus will be turns toward the intact side independent of target position. Unilateral pro-, meso-, and metathoracic legs of a specimen were therefore amputated at different points along the leg and the specimen was then tested for its ability to localize the direction of a surface disturbance.

Distal Tarsal Amputation. When the site of amputation is just proximal to the terminal leg joint (the "joint" between tarsomeres), thus removing the pretarsus and distal half of the tarsus, there is no change in the ability to localize a target placed ipsilateral to the amputation (Fig. 2). The regression line computed for this data (excluding points in the lower quadrant whose target deviation is greater than 120°) is indistinguishable at the 95% level from the regression line computed in a similar manner for the intact preparations. Therefore, the receptor mediating orientation cannot be located in the most distal leg segments.
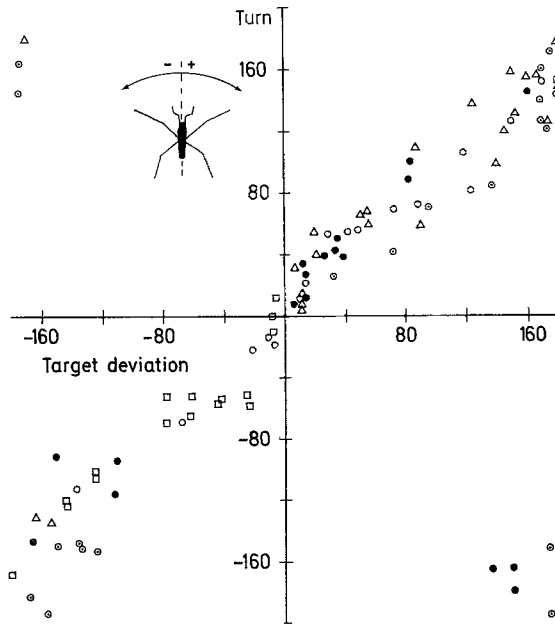
Fig. 1. The relationship between target deviation and turn in tethered preparations. Different symbols indicate different preparations. The diagrammatic representation of the animal relates to the orientation of the axes. Points representing turns toward a target have similar signs. Turns away from a target have unlike signs. 0° is directly ahead, 180° directly behind. A movement which does not change the angular orientation of the longitudinal body axis is a 0° "turn". The units on both axes. These conventions are followed in other figures of a similar nature which appear below

Distal Tibial Amputation. Amputation of unilateral pro-, meso-, and metathoracic legs just proximal to the tibio-tarsal joint disrupts orientation. When the target is ipsilateral to the amputations, the majority of responses are turns away from the target (i.e. toward the intact side, Fig. 3). The receptors important to orientation must therefore be located in the most distal portions of the tibia or the first tarsal subsegment and are probably associated with the tibio-tarsal joints.

When the target is ipsilateral to the intact receptors, the turn elicited by a stimulus is normally correlated with target position (Fig. 3, lower left quadrant). Therefore, whatever parameter of the stimulus is important to determination of the position of the stimulus source, it can be analyzed correctly by a unilateral group of receptors.

Two observations support the conclusion that the results are due to disruption of a sensory system and are not due to some less specific effect. First, since unilateral amputation of the terminal leg segment has
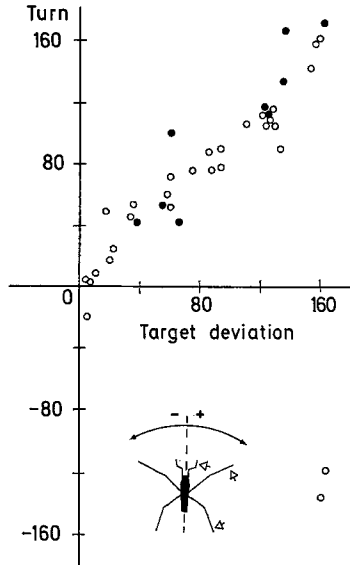
Fig. 2. The lack of effect of amputation of the distal tarsus and pretarsus of a unilateral trio of legs. The open arrows on the diagrammatic animal indicate the legs amputated and the approximate position along the leg. These preparations were tested ipsilateral to the amputation only
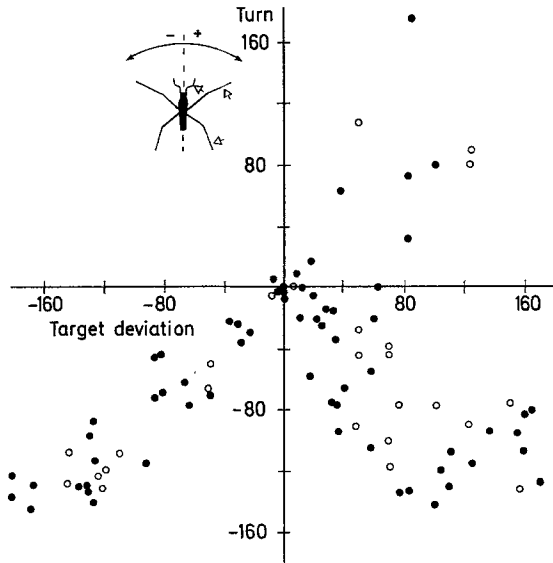

Fig. 3. Errors in orientation induced by amputation of an ipsilateral trio of legs just proximal to the tibio-tarsal joint. The open arrows on the diagram of the animal indicate the legs amputated

no observable affect on the orientation behaviour we cannot conclude that amputation *per se* alters the behavior. Second, the observed disruption of orientation cannot be attributed to changes in locomotor ability. If the amputated legs were not exerting force properly on the water surface, one would expect the largest changes to occur when the target was contralateral to the amputation. For example, the power-stroke of the mesothoracic leg is crucial to turning (Murphey, 1971). Amputation of a mesothoracic leg should greatly affect turns away from this leg if the changes were due to disruption of normal locomotion. This is clearly not the case. The motor response to targets placed on the animal's intact side are normally correlated with target deviation (Fig. 3, lower left quadrant). The regression line computed for target deviations ipsilateral to the intact receptors is indistinguishable, at the 95% level, from the regression line calculated for intact preparations. The observed changes in behavior, upon amputation of the distal tibia, must therefore be associated with alterations of sensory input.

The Role of Individual Receptors in the Control of the Motor Response

The localization of a receptor important to orientation allows further analysis of the nature of the system controlling orientation. A series of amputation experiments were carried out in an attempt to determine the nature of the interactions between sensory input from different legs.

It became clear very early in these experiments that the direction in which an animal would turn could be predicted by making a few very simple assumptions. The assumptions were as follows: 1. The receptors responsible for eliciting orientation are completely non-directional, 2. there is a mechanism by which the CNS can determine the leg nearest the stimulus, and 3. the direction of turning depends solely on the leg nearest the stimulus (i.e. if it is a right leg the turn will be toward the right). On the basis of these assumptions, a simple geometric construction allows the prediction of the direction of turning for any target deviation and any combination of amputations. The method is illustrated in Fig. 4. On the basis of the experiments just described, the receptor is thought to be located at the tibio-tarsal joint. A line is drawn through the joint of the two legs nearest the amputated leg, in this case the left metathoracic leg and the right mesothoracic leg. The perpendicular bisector of this line intersects the circle of target positions at some point ipsilateral to the amputation (138°). When the target deviation is less than this value, the target is closest to the right mesothoracic leg and the preparation should turn right. When the target deviation is greater than this, the target is closest to the left metathoracic leg and the preparation should turn left. A similar construction can be made for any other amputation or combination of amputations.
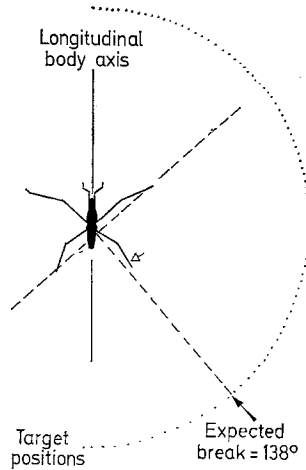
Fig. 4. Diagrammatic explanation of a hypothesis which predicted some of the results and aided in the design of experiments. See explanation in the text

Clearly this method depends on the posture of the specimen being considered. In fact, the posture of individual specimens was not recorded and all predictions were made on the basis of the "average" posture shown in Fig. 4. The posture diagrammed was constructed on the basis of still photographs of preparations at rest on the water surface and the films used in analyzing the motor response (Murphey, 1971).

The Metathoracic Receptor. On the basis of this hypothesis, amputation of a single metathoracic leg should cause the preparation to switch from turns toward the target to turns away from the target at a target deviation of 138° ipsilateral to the amputation (Fig. 4). The fit between the observed result and the predicted result is acceptable (Fig. 5, right hand quadrants). Target deviations greater than 138° ipsilateral to the amputation nearly always elicit turns away from the target. In effect, the point at which an animal would naturally switch from right to left turns has been shifted from 180° to 138° ipsilateral to the amputation.

It is significant that near the expected boundary between right and left turns (Fig. 5, double arrows on the abscissa) all turns are greater than 50° in extent. This suggests that when the stimulus is symmetrically placed between a pair of contralaterally situated receptors, the system responds as if only one of the receptors is being stimulated. The parallel situation occurs in normal animals when the target deviation is near 180°. Under these circumstances, the direction of turning is unpredictable but the size of the turn is always greater than 120° (Fig. 1). Since no small turns occur in either case, one must conclude that the system does not
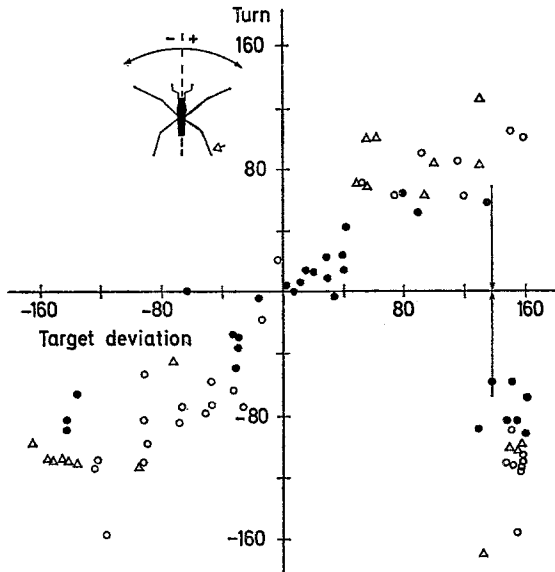
Fig. 5. Errors in orientation induced by amputation of a single metathoracic leg just proximal to the tibio-tarsal joint. The open arrow on the diagram of the animal indicates the leg amputated. The double arrows placed at approximately 140° represent the predicted break between "correct" and "incorrect" turns as explained in the text and in Fig. 4

simply sum the input from contralateral receptors. Rather it selects at random one or the other possible responses and excludes the other completely.

When unilateral pro- and mesothoracic receptors are amputated, the metathoracic input is played off against inputs of the intact side (Fig. 6). Responses are approximately normally correlated with target deviations in the range 80–140° ipsilateral to the amputation (and of course are normal on the intact side). However, at other target deviations, the responses are either directed away from the target (points in the lower right quadrant) or the angular component is larger than expected (points to the left of the double arrows, upper right quadrant, compare with Fig. 1).

There is clearly a range of target deviations in which the metathoracic input is most effective in eliciting a turn toward the target (80–140°). Within this range no turns away from the target occur. This was expected, and the predicted lower end of this range is not too far off (58°). The theory further predicts that the upper end of this range should be 180°. However, the results for intact animals indicate that a fairly large
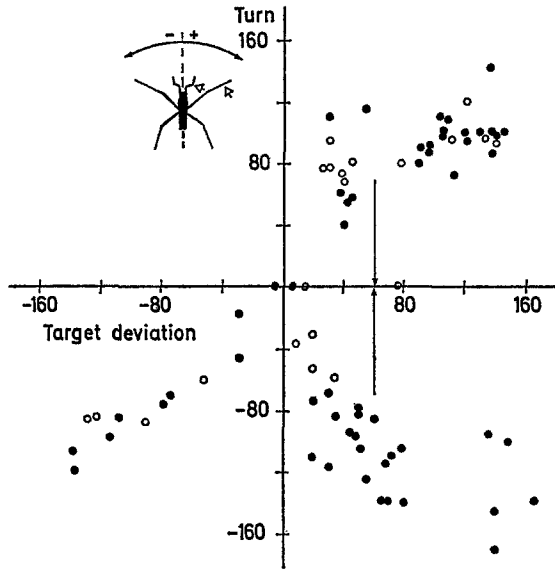
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Fig. 6. Errors in orientation induced by amputation of a pro- and mesothoracic leg just proximal to the tibio-tarsal joint. Open arrows on the diagram of the animal indicate the legs amputated. The double arrows on the x-axis are referred to in the text

error in the direction of turning is tolerated when the target deviation is large (e.g. Fig. 1, solid circles), and the observed switch to turns away from the target at approximately 140° might be attributed to this. The points in the upper quadrant to the left of the double arrows simply cannot be accounted for. It is worth noting that these turns are larger than those produced by intact preparations in response to similar target deviations (see Fig. 1).

The Mesothoracic Receptor. When ipsilateral pro- and metathoracic receptors are amputated, the mesothoracic input is set off against the influence of the contralateral inputs. Under these conditions the theory predicts that turns toward the intact mesothoracic leg will occur only inside the range 10–138° ipsilateral to the amputations. The observations are in reasonable agreement with the predictions (Fig. 7).

The mesothoracic receptor was also used as an example in an experiment designed to demonstrate the role of the contralateral inputs on the motor response elicited by a given receptor. All but the mesothoracic legs were amputated just proximal to the tibio-tarsal joint. The preparation was then tested for its response to targets ipsilateral to the intact leg (Fig. 8). Clearly the contralateral inputs have a negative influence on the torque produced by stimulation of the mesothoracic leg (compare
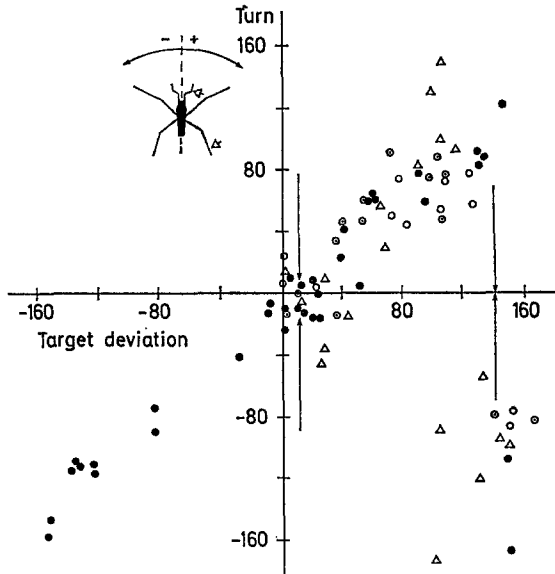
Fig. 7. Errors in orientation induced by amputation of a pro- and metathoracic leg just proximal to the tibio-tarsal joint. The open arrows indicate legs amputated. The double arrows on the x-axis are referred to in the text
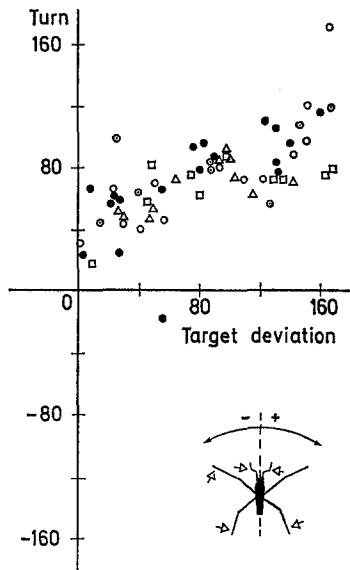

Fig. 8. Turns observed when a single metathoracic leg is intact and the target is ipsilateral to the intact leg. These results should be compared with the right-hand quadrants of Fig. 7. There is a slight but significant (95% level) slope to the results. The appropriate results of Fig. 11 are included here
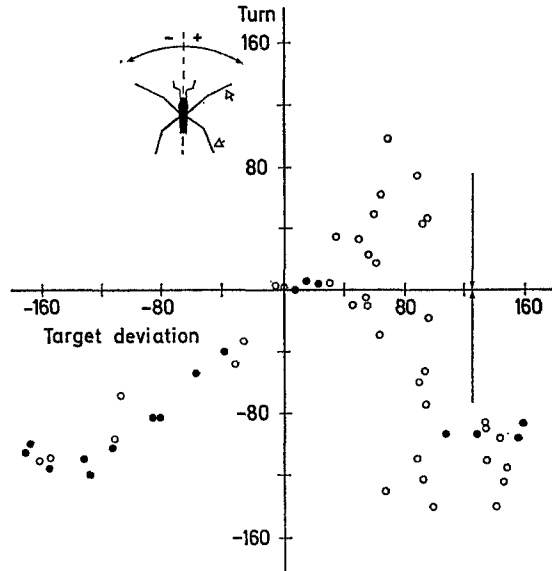
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Fig. 9. Errors in orientation induced by amputation of a meso- and a metathoracic leg. The amputations are just proximal to the tibio-tarsal joint (open arrows on diagram of the animal). The double arrows on the x-axis are referred to in the text

Fig. 7, right hand quadrants, and 8). This negative effect is most pronounced when the target deviation falls in the range of target positions which produce "incorrect" turns when the contralateral legs are intact (0–10° and 138–180° ipsilateral to the intact leg). Without the contralateral input turns are always directed toward the target (when the target is ipsilateral to the intact leg). At small target deviations the turns are larger than those obtained when the contralateral legs are intact.

    The Prothoracic Receptor. A preparation with amputations of an ipsilateral pair of meso- and metathoracic legs demonstrates the influence of the prothoracic receptor when it is opposed only by contralateral inputs. The directionality of the response switched from turns toward the target to turns away from it at approximately 100° ipsilateral to the ablations (Fig. 9), in other words, short of the predicted value by 15°.

    Direct tests of the effect of prothoracic input on motor output were not successful because preparations lacking all but a prothoracic receptor were very unresponsive. The role of prothoracic inputs is therefore inferred on the basis of Figs. 3 (intact side), and 10 (open circles). It was pointed out earlier that unilateral amputees respond normally to targets ipsilateral to the intact receptors (Fig. 3, intact side). However, a similar preparation which lacks the prothoracic receptor of the "intact" side

as well (Fig. 10, open circles) tends to overshoot the target at small target deviations. Therefore, the prothoracic input appears to have a negative influence on the torque which is elicited by stimulation of the ipsilateral meso- and metathoracic legs.

Interaction of Ipsilateral Inputs. The results presented thus far indicate that each tibial receptor functions most effectively over a restricted set of target positions. The evidence just presented suggests that the prothoracic input has a negative influence on the torque which might be elicited by stimulation of the receptors of ipsilateral legs. The following experiment was carried out to test further the interaction of ipsilateral inputs. If the input from two ipsilateral receptors can be summed it is most likely that such summation would occur when a large turn is required, i.e. at large target deviations. Therefore, a preparation retaining only ipsilateral meso- and metathoracic receptors was tested for its response to target positions ipsilateral to the intact legs. The meso-thoracic leg was then amputated and the preparation tested again. If the inputs from the two legs summate at some point in the system the removal of one of the remaining inputs should depress the response.

Preparations retaining only meso- and metathoracic inputs tend to overshoot the target at small target deviations due to the lack of the prothoracic receptor (Fig. 10, open circles). When the remaining meso-thoracic leg of the *same* preparation is amputated, there is a tendency to overshoot even further at small target deviations (Fig. 10, solid circles) indicating again the negative effect of a receptor on a more posterior (and ipsilateral) neighbor. The most significant finding, however, was the similarity of the turns produced at large target deviations whether the mesothoracic input was intact (open circles) or not (solid circles). This indicates that summation is not required to produce the observed responses. Therefore, the only interactions which can be demonstrated to occur between input from different legs are negative in sign.

Single Receptor Input. The experiments presented above indicate that the receptor of each leg in the intact preparation is "responsible" for eliciting turns toward targets over a particular range of target positions. Furthermore, there is some evidence to suggest that the size of the turn elicited by stimulation of a given receptor is dependent on the segment in which the receptor is located. In order to test this possibility further, a single mesothoracic leg was left intact and all other legs were amputated just proximal to the tibio-tarsal joint. The preparation was then tested for its ability to localize the direction to the stimulus source. The amplitude of the ripples at the tibio-tarsal joint of the intact leg was held constant by keeping the distance from the source to the leg constant.

A large portion of the turns elicited under these conditions were of intermediate size and, as expected, most of the turns were directed
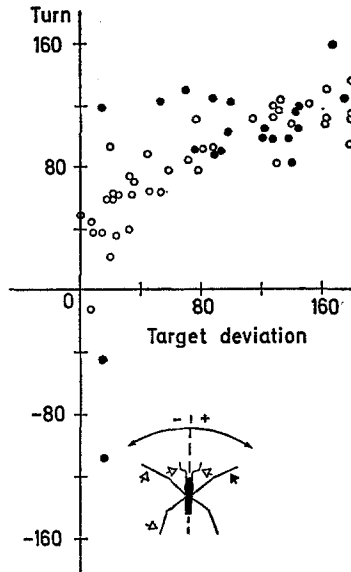
Fig. 10. The relationship between ipsilateral meso- and metathoracic receptor inputs. Initially, amputations were made just proximal to the tibio-tarsal joint of four legs (open arrows on diagram of the animal). Therefore, the open circles represent the responses of the preparation possessing only an intact meso- and metathoracic leg. The remaining mesothoracic leg was then cut and the same preparation tested again (solid circles). The preparation was tested only for its responses to targets ipsilateral to the intact legs

toward the intact leg (Fig. 11). However, there is a significant positive correlation between target deviation and turn when all the results for such preparations are considered together (Fig. 8, ipsilateral target deviations only). The simplest hypothesis: namely, that input from a given leg will elicit a turn of some constant magnitude dependent only on the segment with which the leg is associated, must therefore be rejected. The most that can be said is that input from a given leg will elicit a characteristic output (turn) but this output is related to target deviation as well as to the segment with which the intact leg is associated. This may indicate that the receptors being examined are slightly directionally sensitive.

It was unexpected that a large proportion (14/34) of the responses should be directed toward the target when the target was contralateral to the intact leg (turns in the lower left quadrant of Fig. 11). A similar although less pronounced (10/40) result was obtained for unilateral distal tibial amputees (turns in the upper right quadrant of Fig. 3). There are two possible explanations for these results: either the receptor under
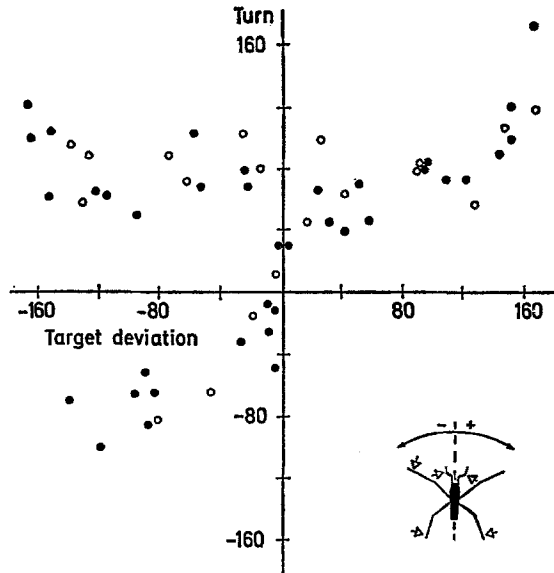
Fig. 11. Orientations by preparations with amputations of all but a single mesothoracic leg. Positive target deviations are ipsilateral to the intact leg

consideration is not being completely blocked by the ablation or other receptors feed into the system controlling orientation.

The experiment involving amputation of all but a single leg demanded that the system be tested at target deviations which completely encircled the animal while keeping the amplitude of the stimulus applied to the intact leg constant. Under these conditions, target deviations contralateral to the intact leg would stimulate the amputated legs much more intensely than the intact legs. Due to the damping of surface ripples of the required size and frequency an amputated mesothoracic leg would receive a stimulus 2–3 times greater in amplitude than the intact leg when the target was contralateral to the intact leg. It would therefore be legitimate to argue that the threshold of the receptor under consideration has simply been increased and the increased amplitude of the stimulus partially compensates for this change. It would be equally legitimate to argue that a second set of receptors with a somewhat higher threshold than those ablated is brought into action by the more intense stimulation.

Unpublished experiments eliminate the first alternative. Extracellular recordings from tibial leg nerves demonstrate that there are receptors, associated with the tibiotarsal joint, which respond vigorously to the stimulation used in these experiments. The response of these

receptors is completely blocked by amputation just proximal to the tibio-tarsal joint. Therefore, it must be concluded that there exist receptors other than those located at the tibio-tarsal joint which are involved in the control of orientation to prey.

Discussion

Every predator has three tasks it must perform if it is to survive. It must detect prey, locate, and capture it. The manner in which organisms are able to "decide" where in their environment a stimulus is and take appropirate action has therefore been studied in a number of predators (e.g. the preying mantis, Mittelstaedt, 1957, and jumping spiders, Land, *in Press*). An analysis of the prey capture behavior of the waterstrider has provided some insight into the manner in which this species has solved the problem of coordinating patterns of sensory input with appropriate motor responses.

The Receptor System. Orientation to a stimulus usually depends on the directionality of the receptors, the comparison of stimulus parameters between bilaterally situated receptors, or some combination of these two mechanisms. The behavioral evidence presented here indicates that the receptors examined in these experiments may be slightly directionally sensitive (Figs. 8 and 11). Localization of a stimulus in this system, however, seems to depend on the animal's ability to determine which of the six legs is closest to the stimulus.

Such a determination might depend in this case on the amplitude of the ripples. Van Bergeijk (1967) has suggested that the amplitude of surface ripples might be the most relevant stimulus parameter to an organism trying to determine the direction to a source of ripples. The anatomy of waterstriders is well suited to such a mechanism. The distances between the tibio-tarsal joints of adult specimens are, with the exception of the distance between the two prothoracic legs, greater than 2 cm. Since surface ripples in the appropriate frequency range damp to half-amplitude in 2–4 cm, it is clear that for most target positions one leg will be receiving much more intense stimuli than any of the others. The data presented here do not eliminate the other stimulus parameters which might be used to determine the leg nearest the stimulus; namely, time of arrival and phase. However, phase relationships may be eliminated theoretically because the wave lengths of the ripples will in many instances be short enough to allow nearly any phase relationship at a given pair of receptors, depending only on the frequency.

Whatever the relevant stimulus parameter is, it does not require bilaterally symmetrical receptors for detection and analysis since uni-

lateral distal tibial amputees can make turns appropriate to the stimulus position when the stimulus is ipsilateral to the intact legs (Fig. 3).

The Motor System. The analysis of the motor response provides some insight into the functioning of the control system underlying orientation. Data obtained from extracellular recordings of motor neuron activity in tethered animals (Murphey, 1971) cannot be interpreted as being due to monosynaptic reflexes. Thus it is concluded that in some way inter-neurons receive and analyze the information concerning the direction of a source of ripples and the activity in this group of interneurons then releases a coordinated motor response appropriate to the pattern of the sensory input. The probability that interneurons control the behavior is supported by the observation that motor neurons which are synchronized during certain movements show parallel changes in firing rate, suggesting a common driving interneuron (e.g. Fig. 8, contralateral target positions, Murphey, 1971).

Central Interactions. There is a good deal of evidence suggesting inhibitory interactions between receptors at some level of the CNS. When certain combinations of contralateral receptors are stimulated symmetri-cally, the motor response which occurs is characteristic of stimulation of one or the other of the legs being stimulated and is never some inter-mediate value. For example, when the target is directly behind the animal the right and left metathoracic receptors are equally stimulated but the motor response is always a large turn to the left or the right, never a movement aimed directly ahead as might be expected when bilaterally symmetrical receptors are stimulated. Similarly, when a metathoracic receptor is removed by amputation and the target placed symmetrically between the mesothoracic receptor ipsilateral to the amputation and the remaining metathoracic receptor (Fig. 5), the re-sponses to stimuli are characteristic of either the stimulation of a meso-thoracic leg or stimulation of a metathoracic leg but seldom an inter-mediate value (e.g. target positions near 138° in Fig. 5). This implies that the inputs tend to exclude one another. The evidence bearing on the interaction of ipsilateral inputs indicates that these are also inhibitory interactions (see the discussion of the results of Fig. 10).

The working hypothesis utilized in the design and analysis of many of the experiments reported here is inadequate in many respects. On the motor side, the extent of the turn in a given situation is ignored by the model, which predicts only the direction of turning. As a consequence of this shortcoming the model provides no insight into the manner in which the continuous relationship between target deviation and the turn is produced. On the sensory side the model assumes that the receptors are completely non-directional, an assumption which is questioned by the results of experiments in which only a single receptor is left intact (Fig. 8

and 11). Furthermore, the receptors are assumed to be localized at the tibio-tarsal joint only. In fact, it was pointed out earlier that other receptors, located proximal to this joint, must also be involved in the control of orientation to prey.

Since these inadequacies cannot be readily resolved with the data at hand, it seems premature to present yet another model. However, it may be worth summarizing the points future analyses will have to take into account in attempting to model this system. First, central inhibition between inputs should be incorporated into any further attempts to model the system. Second, some method of predicting the extent of turning expected under different experimental conditions must be introduced if the model is going to be useful. Finally, the continuity of the relationship between target deviation and turning response will be an important aspect of future models.

Feedback during Turning. A system which is similar in many respects to the one controlling orientation in *Gerris*, the response of jumping spiders to a moving stimulus impinging on the postero-lateral eyes, is an open—loop system. The tendency for these animals, as with *Gerris*, is to align the stimulus with the longitudinal body axis, and in this case examine it more closely with the more sophisticated anterior eyes. The control of the turning movement does not depend on the stimulus once the movement is initiated (Land, 1969 and in Press).

The control of turning by gerrids may be an open loop situation as well, although it has proven difficult so far to obtain open loop conditions in these experiments. Preparations tethered tightly enough to allow leg movement but not actual changes in body orientation, a good way to block feedback during the movement, do not respond to surface ripples. Nevertheless, a few facts support the suggestion that the system controlling orientation is an open loop.

Since the receptors are located in the legs, it is difficult to imagine how receptors could receive any stimuli during a movement. This is particularly true in the case of the mesothoracic receptor which is not only moving rapidly during a powerstroke but is presumably blocked by the relatively violent stimuli it must receive when the motor movement occurs. Furthermore, orientation occurs as a series of discrete turns followed by distinct intervals where no leg movement is made (usually greater than 200 msec). It seems very likely that these pauses allow determination of the "new" target position after a turn.

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