J. comp. Physiol. 84, 31—40 (1973)

Mutual Inhibition and the Organization of a Non-Visual Orientation in *Notonecta*

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Received January 30, 1973

Summary. 1. Hypotheses concerning the neural mechanisms by which the back swimmer *Notonecta undulata* locates prey have been examined using behavioral tests.

2. The results are consistent with the following hypotheses: A. The receptor nearest the target controls the direction of the turn which is elicited by a stimulus (Figs. 2 and 3). B. Sensory input via a given receptor is capable of eliciting a very limited range of motor responses (Fig. 3). C. There are inhibitory interactions between receptors at some level of the central nervous system (Figs. 6 and 7C).

3. A neuronal network analogous to a lateral inhibitory network is proposed to be the neural basis for the orientation (Fig. 5).

Introduction

Lateral inhibition, first demonstrated in the visual system by Hartline (1949), appears to be a common feature of sensory systems which encode location of the stimulus with respect to the receptor array. Crossed inhibition between bilaterally placed pairs of neurons thought to be crucial to orientation has been described in insect auditory systems (Suga, 1963; Katsuki and Suga, 1961; McKay, 1969). Inhibition appears to be equally important for stimulus localization in the tactile (Mountcastle, 1961) and auditory senses of vertebrates (Moushegian *et al.*, 1964; Rose *et al.*, 1966).

The preceding paper demonstrated that the aquatic bug *Notonecta undulata* accurately locates the source of surface ripples through a vibration sense. Back swimmers (*Notonecta* sp.), waiting for prey, float against the under side of the water's surface with only five points in contact with the surface film; the tips of the four anterior legs and the tip of the abdomen. There are six receptors associated with these five points, one in each leg and two associated with the tip of the abdomen. Three basic and inter-related hypotheses about the control of orientation have been examined. First, it is hypothesized that the receptor nearest the target determines the direction, right or left, toward which the turn will be directed. Second, each receptor is assumed to be capable of triggering turns of one size. Third, inhibitory interactions which occur within the central nervous system provide the gradation necessary to produce the linear input-output relationships which is observed.

The results of experimental alterations of the sensory input through ablation support the conclusion that the linear relationship between target angle and turn depends on central inhibitory interactions between input from different receptors. This demonstration combined with a number of other reports, suggest that all animal orientations, independent of sensory modality, are based on mutual inhibitory networks.

The *methods* are described in the preceding paper (Murphey and Mendenhall, 1973).

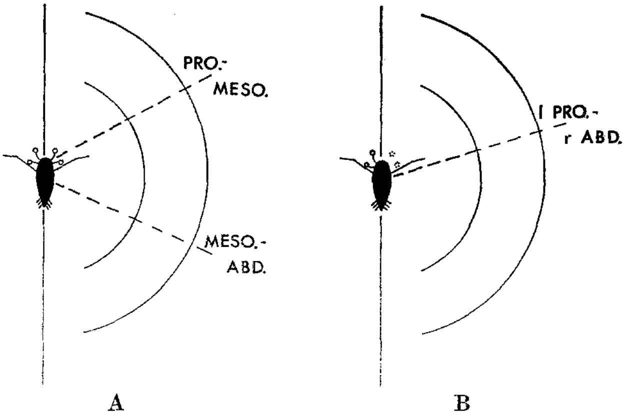

Fig. 1A and B. A geometric analysis of the positions of the sensory receptors and their relationship to target position. The dashed lines indicate the boundaries between regions nearest one receptor and those nearest an adjacent receptor. A. Intact specimen. B. A specimen with the pro- and mesothoracic receptors of the left side ablated

Results

Turn Direction Determined by the Receptor Nearest the Target

The geometry of the situation is such that the perpendicular bisectors of the lines connecting adjacent points of sensory input (i.e., adjacent as you go around the animal) partition the space surrounding the animal into six approximately equal segments corresponding to anterior-lateral, lateral, and posterior-lateral on each side (Fig. 1A). A target anywhere within one of these 60° segments will be nearer the receptor for that segment than it will be to any other receptor. If it is assumed that the receptor nearest the target determines the direction of a turn, then obviously the midline will be the boundary between right and left turns in

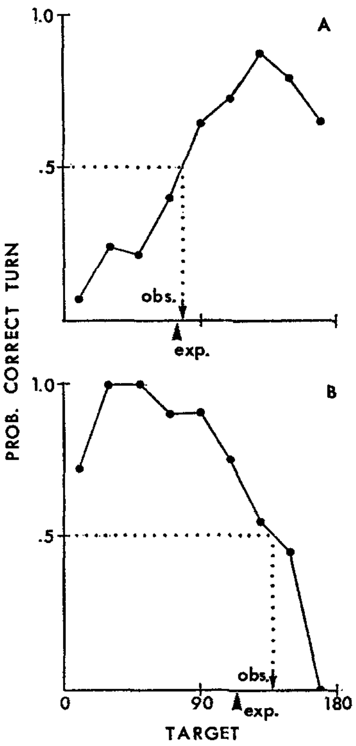

Fig. 2A and B. Predicted and observed boundaries between correct and incorrect turns in two ablation experiments. The boundary is defined as the point at which 50% of the turns are directed toward the target (correct) and 50% are directed away from the target (incorrect). A. Unilateral leg receptors ablated, four specimens represented. B. Unilateral abdominal receptors ablated, two specimens represented. The graphs refer to target positions ipsilateral to the ablations only. The dotted lines indicate the observed 50% point, the large arrowhead indicates the expected value

normal animals. The boundaries between correct and incorrect turns can be predicted for various additional experiments by constructing the perpendicular bisector of the line between the receptors which *become adjacent* due to ablation. For example, ablating the pro- and mesothoracic receptors unilaterally makes the abdominal receptor of the lesioned side and the intact prothoracic receptor adjacent (Fig. 1B). The perpendicular bisector of a line between these two receptors is equal to a target position of 75° and the ablation should lead to incorrect (directed away from the target) turns in the range 0–75° ipsilateral to the lesions but correct turns for target angles 75–180°.

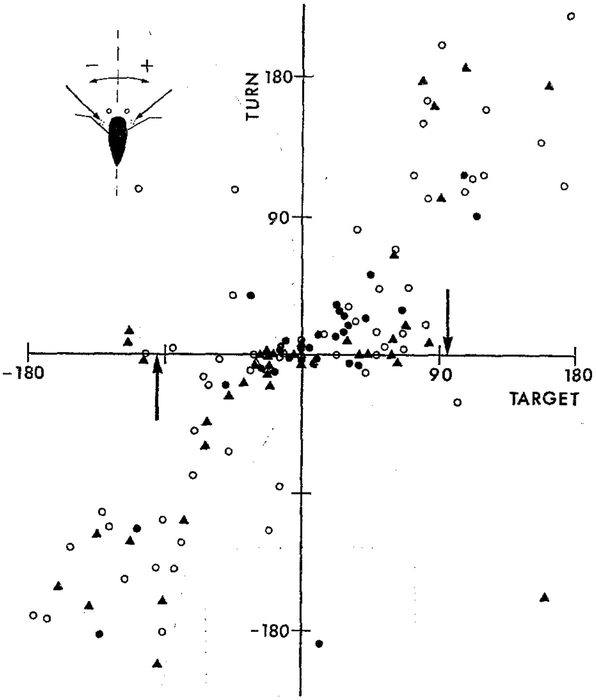

Fig. 3. A step function induced by ablation of the mesothoracic receptors. The arrows indicate the target position at which the switch from small to large turns is expected to occur. Individual specimens are indicated by different symbols

This aspect of the model was tested in three ablation experiments. First, unilateral ablation of pro- and mesothoracic receptors caused specimens to turn away from a target when the target was ipsilateral to the ablation, except when the target angle was large. The observed switch from incorrect to correct turns occurred at 80° (Fig. 2A), the predicted value was 75°. Second, when the abdominal hairs were ablated unilaterally the switch from correct to incorrect turns for targets ipsilateral to the ablation occurred at approximately 140° (Fig. 2B), the two specimens tested, bracketed (110° and 160°) the expected value of 115°. A third case, discussed in more detail below, is the prediction that a "step" from small to large turns will occur at approximately 95° if the mesothoracic receptor is ablated: The observed value was 80° (Fig. 3). The consistency of prediction and observation implies that the central nervous system determines which receptor is nearest the target, since that is the assumption implicit in the geometric analysis, and then makes a turn of the appropriate direction.

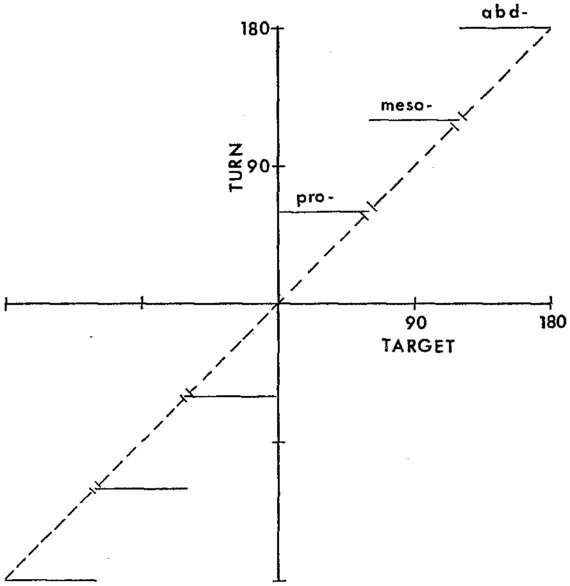

Fig. 4. Hypothetical step function underlying the orientation response. The solid lines indicate the maximum size turn which can be elicited by each receptor. The dashed line indicates the response of normal specimens

Stimulation of One Receptor Elicits One Size Turn

If the model is extended by assuming that each receptor can elicit a single size turn—small, medium, or large—corresponding to receptor position, then the expected input-output relationships is a step function with three levels corresponding to prothoracic, mesothoracic, and abdominal input (Fig. 4, solid lines). The positions at which the step to a new level occurs are predicted by the geometric constructions of Fig. 1 A. For example, the boundary between medium and large turns is the perpendicular bisector of a line connecting the mesothoracic and abdominal receptors (120°, Fig. 1 A).

Two experiments demonstrated that a step function is basic to the normal response. First, unilateral ablation of the leg receptors removes all input to the lesioned side except that from the abdominal hairs. It was demonstrated in the preceding paper that the turns toward the target elicited by the remaining intact abdominal receptor were large (>100°), and showed no evidence of gradation appropriate to target position. Thus, when input to the abdominal receptor alone triggers a turn, that turn has a constant size irrespective of target position. Second, removal of both mesothoracic receptors converts the linear relationships between target position and turn to a step function (Fig. 3). The size of the turns falls into two classes, small and large, as expected on the basis of removal of the middle level in Fig. 4. The step from small to large turns occurs in the middle of the range of target positions (approx. 80°) as expected on the basis of a geometric analysis analogous to those shown in Fig. 1. Thus it appears that stimulation of a given receptor elicits a limited range of motor responses.

Inhibition as a Mechanism for Gradation of Turn Size

In spite of this demonstration, the fact remains there is very little evidence for a step function relating target position and turn size in the results for intact specimens. The turning response varies uniformly with target angle except when the target is directly behind the animal. This suggests that "central interaction" between inputs from different receptors are involved in converting the step function (Fig. 4, solid lines) into a continuous function (Fig. 4, dashed line).

Two preliminary observations suggested that the required interaction is an inhibitory one. When two competing responses are possible (e.g., right versus left turn when the target is directly behind the specimen), one response always cancels the other. On the basis of this result, and results in a related insect (Murphey, 1971), a hypothesis was constructed which included mutual inhibition between all sensory inputs at some level of the central nervous system.

The simplest system compatible with all results presented thus far is one in which each receptor drives a command interneuron, and each command interneuron is capable of eliciting turns corresponding to a small portion (approximately one-third) of the total range of possible turn sizes (Fig. 5). For example, the prothoracic receptor would drive a command cell which was capable of eliciting turns of 0–60° in size. Within this range, variations in command cell firing rate would vary the size of the turns between 0 and 60°. If the command cells were part of a mutual inhibitory network, then the required gradations of command cell firing rates – and thereby turn size – might be obtained. Range fractionation of a motor output has been demonstrated by Davis and Kennedy (1972) in command cells for swimmeret beating in lobsters.

If a lateral inhibitory network is present in the control system underlying this behaviour, then removal of a receptor should have predictable effects on the input-output raltionship for the behavior. The simplest experimental test for this type of interaction would be removal of a receptor between two others, all of which elicit turns in the same direction (only the mesothoracic receptor fits this requirement). Ablation of the mesothoracic receptor should disinhibit the proposed abdominal and prothoracic command neurons in the region of target angles usually accounted for by mesothoracic input. Specifically, turns should be either larger or smaller than normal in the range of target

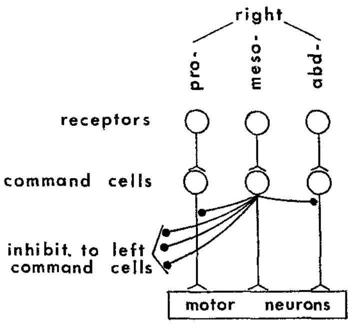

Fig. 5. The neural circuit hypothesized to be controlling the orientation behavior. (See text for details)

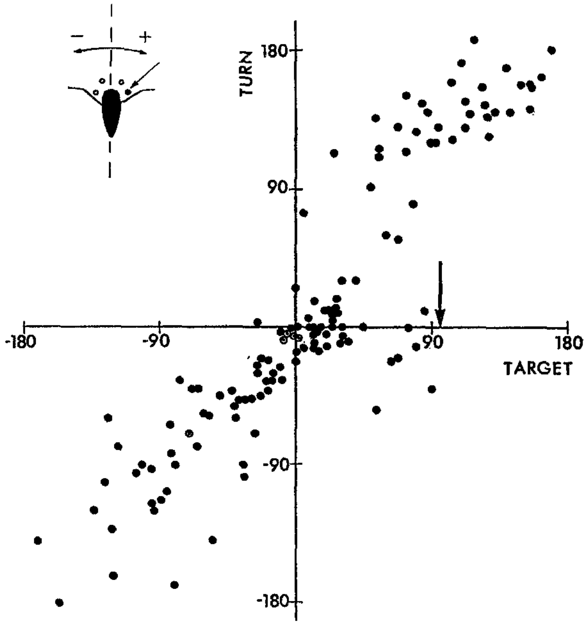

Fig. 6. Overshoot at intermediate target angles induced by unilateral mesothoracic receptor ablation. The arrow indicates predicted boundary between small and large turns on the lesioned side

angles 60–120°. This experiment was carried out in two ways. First, both mesothoracic receptors were ablated and the results were compared with intact animals. Second, one mesothoracic receptor was ablated and the intact side was used as a control. The two experiments are really quite different in terms of the alterations in the pattern of input the

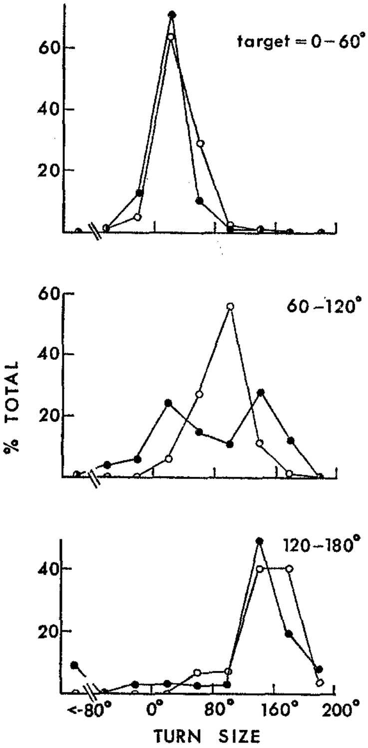

Fig. 7. Turn size as a function of target position for unilateral mesothoracic ablation. Each graph indicates the per cent of turns of a given size made in response to targets in the range indicated at the right. The open circles are the results for the intact side. The filled circles are the ablated side. Three specimens, including the one shown in Fig. 6, are represented; each contributing approximately the same number of data points. Note that the ablation induced differences only in the middle portion of the range of target angles (60–120°) and that turn size is bimodally distributed in this way

central nervous system must receive during a stimulus: in the first case the input remains bilaterally symmetric and in the second case an asymmetry is induced.

The results are essentially the same in both cases. Animals tend to overshoot or undershoot in the middle portion of the range of target angles (Figs. 3 and 6). More specifically, turns to target angles in the range 60–120° ipsilateral to an ablated receptor are bimodally distributed and as predicted the two modes bracket the results for the intact side (Fig. 7B). Over the remainder of the range of target angles the responses for the intact and lesioned sides are indistinguishable (Figs. 7A and 6). Note that the two modes in Fig. 7B correspond to the expected values for smaller or larger target positions (Fig. 7 A and C). The results are the same for bilateral mesothoracic lesions (Fig. 3) although there is less variability in the response of these specimens than in the unilaterally lesioned specimens. Thus it is concluded that an inhibitory network similar to the one diagrammed in Fig. 5 is an integral part of the mechanism controlling orientation to prey.

There is another way to test aspects of these hypotheses. When a prothoracic receptor is ablated, small turns should be eliminated for targets ipsilateral to the lesion (i.e., removing the prothoracic step and extending the mesothoracic step to the y-axis in Fig. 4). The mesothoracic command cell should be disinhibited and the specimen should overshoot targets between 0 and 60° ipsilateral to the lesion. Similarly, bilateral prothoracic ablation should lead to overshooting between 0 and 60° and an abrupt step from right to left turns at the origin.

The results from experiments with prothoracic lesions were inconclusive. In some (approximately 50%) preparations, the expected overshoot at small target angles occurred; in others it did not, and always the differences were very subtle. The results are not perfectly consistent with the hypothesis, and modifications in the model which might be used to account for this result will be considered in the discussion section.

Discussion

Throughout this description it has been assumed that the input to the central nervous system provided by each receptor is equally weighted in terms of its effect on motor output. The results for prothoracic ablations suggest that there are differences in the importance of each receptor in the overall response. The prothoracic receptor, which was demonstrated to be capable of eliciting small turns (Fig. 3), can apparently be dispensed with and the interactions between remaining receptors will lead to a nearly normal input-output relationship. The simplest change in the model which might account for these results is to assume that the mesothoracic command interneuron is capable of gradation of turns from 120° down to 0° rather than 120° down to 60° as proposed in Fig. 4. Removal of a prothoracic receptor would alter the normal input pattern but the inhibition from the remaining receptors would be sufficient to depress mesothoracic command cell firing rates to a point appropriate to small turns.

The hypothetical neuronal network used to design these experiments was constructed in analogy to the lateral inhibitory network of the *Limulus* eye. "Adjacent" receptors were defined as adjacent in a radial sense—moving around the animal. Thus, the coefficient of inhibition (r in Hartline and Ratliff's 1957 formulation) should decrease as one moves around the animal away from a given receptor. However, the results for prothoracic ablations indicate that the inhibitory coefficients do not change with distance "around" the animal. On the basis of the results available, it is likely that crossed inhibitory influences are the most powerful, front to back next, and back to front inhibition the least powerful. This would be consistent with the known organization of segmental inhibitory interactions demonstrated in other Arthropod nervous systems (Suga, 1963; Palka, personal communication; Eckert, 1961).

The behavioral demonstration that inhibition is a basic component of the neural circuitry controlling orientation to surface ripples in *Notonecta* adds to the long and growing list of examples of mutual inhibition in non-visual sensory systems (Mountcastle, 1961; Moushegian *et al.*, 1964; Rose *et al.*, 1966). This widespread occurrence of lateral inhibitory networks found at different levels but always involved in the localization of a stimulus suggests that when comparison of two or more receptors is possible, orientation to a point source of stimulation always depends on some form of lateral inhibition.

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