CENTRAL CONTROL OF AN INSECT SEGMENTAL REFLEX

I. INHIBITION BY DIFFERENT PARTS OF THE CENTRAL NERVOUS SYSTEM

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An earlier paper (Rowell, 1961 *a*) described a reflex cleaning or grooming movement by the front leg in *Schistocerca gregaria;* it is evoked by stimulation of the sensilla of the prothoracic sternum. In the unrestrained animal this response can only rarely be seen, but under experimental conditions it can be obtained reliably if the connectives uniting the prothoracic ganglion to the rest of the c.n.s. are cut, provided that the tarsi of the front legs are not allowed to contact anything. Under all other conditions the reflex is partially or completely inhibited.

The need for central control of 'peripheral' reflexes is especially obvious in insects, with their complex behaviour and segmentally organized nervous system. Some broad conclusions about this control have been reached on the basis of earlier lesion experiments (see Roeder (1953, 1958) for reviews). Successive removal of the supra- and suboesophageal ganglia cause first hyperactivity and then depression of behaviour such as locomotion and of many reflexes, suggesting inhibitory and excitatory functions for these two areas. The terminal abdominal ganglion of many insects is influenced by inhibition from the head ganglia, and inhibitory relations between different thoracic segments are known in the locomotion of insects. Little is known about the mechanism of this control. The inhibition of the prothoracic cleaning reflex in *Schistocerca* is being studied, and the present paper deals with lesion experiments. A brief note on some of the results has been published elsewhere (Rowell, 1963).

Areas evoking the cleaning reflex (see also Fig. 1).

1. Hair sensilla of the sternal spine.
2. Hair sensilla of the sternum proper.
3. Forward-pointing hair sensilla along the anterior thickened margin of the sternum.
4. Coxal membranes—no visible sensilla.
5. Hair sensilla of the coxa and trochanter.

Areas 1, 2 and 3 may produce a response by either leg, or, if the threshold is low, by both legs. Areas 4 and 5 typically produce a response by the leg on the affected side, but the other leg may join in if the stimulus is strong. All these areas are innervated by branches of nerve 2 of the prothoracic ganglion (Rowell, 1961 *a*)*.

* In the 1961 paper I claimed that the number of sensilla greatly exceeded the number of axons and that therefore some fusion of axons must take place. This is wrong. Electron micrographs show 1200–1500 axons in each of the nerves where they join the ganglion, which is enough to account for all the sensilla. Many are small, less than 1 μ diameter, and were not seen with the ordinary light microscope in the earlier sectio--

6. Cervical membrane. The response from this area is mediated by the paired chordotonal organs, which are stimulated by movement of the neck membrane and innervated by a branch of nerve 2 (Rowell, 1961 a). The optimal stimulus is a prod to the ventral part of the stretched neck membrane, and this is a more effective stimulus than 1–5 above, evoking the response after the others have ceased to do so.

7. Hair sensilla of the lateral anterior mesothoracic sternum.

8. Hair sensilla of the pro/mesothoracic intersternal membrane. This area is hidden in normal posture and tonus, but gives a response if artificially exposed and stimulated.
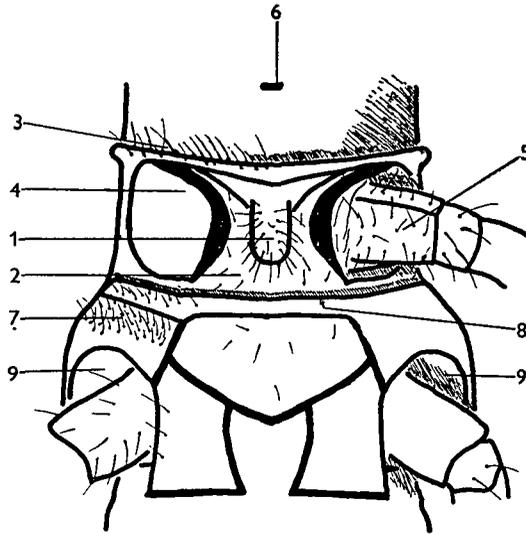

Fig. 1. Ventral view of the pro- and mesothorax of *Schistocerca* showing the distribution of sensilla mediating the prothoracic cleaning reflex. The numbers refer to the list in the text where these areas are discussed.

9. Coxal membranes of the mesothoracic legs (when pricked). This is most effective if the mesothoracic legs, which would otherwise respond, are amputated.

Areas 7, 8 and 9 are all connected to the prothoracic ganglion via the meso/prothoracic connectives and nerve 2 of the mesothoracic ganglion (nomenclature after Campbell (1961) for *Locusta*). They are more effective in eliciting a response than any of the areas served by nerve 2 of the prothoracic ganglion itself.

EXPERIMENTAL TECHNIQUE

The insects used were adult desert locusts (*Schistocerca gregaria* Forskål) of either sex raised in crowded conditions in laboratory culture. Experiments were performed in a quiet room at an air temperature of between 24 and 28° C.

The basic procedure was to isolate progressively the prothoracic ganglion from the rest of the C.N.S., and to measure the responsiveness of the reflex at each stage. The insect was pinned dorsal surface down on a wax block by two pins running obliquely through the metathoracic tergum and by one pin through the frons which kept the neck extended and the mouthparts away from the prothoracic sternal region. The

reflex is inhibited if either of the prothoracic tarsi contact anything; care was therefore taken to avoid placing the pins in accessible positions. The meso- and metathoracic legs were amputated at the trochanter in order to make the preparation suitable for electrophysiological recording in later experiments. Either the anterior or posterior C.N.S. was disconnected from the prothoracic ganglion, by cutting the appropriate connectives, in order to study the effect of the remaining part. The first lesion was then made to the remaining C.N.S. and at least 5 min. were allowed before the first test.

Before the first test both legs were excited into making the response by stimulating the mesothoracic sensilla, area 7. This was a general check on responsiveness and working order, and also avoided starting with different sequential effects for the two legs (see below). After one minute the first test was made. The hairs of the sternal spine were touched with a fine needle (under binocular microscope) and the response of the legs was recorded. Two minutes were then allowed before the second test was made. In this way twenty tests were made for each lesion. After this the next lesion was made, and the procedure was repeated until the lesion series had been completed on that animal.

Some surgical operations proved to be impracticable. It would have been desirable to see the effect of bisecting longitudinally the prothoracic ganglion or other ganglia connected to it. However, section of the prothoracic ganglion invariably damaged the nerves or muscles involved in the reflex, and with the other ganglia I could not get repeatable results. A methodological difficulty is that the effect of the metathoracic ganglion on the prothoracic is obscured by that of the mesothoracic, through which the connexion is made. Attempts were made to cauterize the lateral parts of the mesothoracic ganglion, leaving the central through tracts unharmed, but these were unsuccessful. Accordingly, the effects of the metathoracic ganglion had to be inferred by subtracting the known effects of the mesothoracic ganglion alone from the combined effects of the meso- and metathoracic ganglia. This presupposes additive relations between the latter two, which is unjustified, but the method is here retained as an approximation.

There was found to be a pronounced sequential (?Markovian) effect consequent on performance by the individual leg: if the stimulus is repeated, the leg which responded last time will probably do so again. It was therefore necessary throughout testing to 'set to zero' the responsiveness of the legs at frequent intervals by making sure that they had responded, at least within the last two tests. It is for this reason that both legs were made to respond initially before testing began, and any leg which failed to respond in two consecutive tests was excited to do so before the next test took place. A possible reason for this sequential effect is offered later.

EVALUATION OF THE RESPONSE TO TESTING

(1) *Measures*

The responses of the legs to stimulation were described in two ways.

(*a*) Overall responsiveness was measured by (i) the percentage of responses, i.e. the number of times the locust responded to the stimulus relative to the number of times it was tested, and (ii) the number of leg movements per response. These two measures were throughout highly positively correlated (thus when the locust made many responses it also made many leg movements in each response—the highest average

number reached was about 2·5), and for simplicity's sake only the first measure, the percentage response, will be given.

(b) The number of leg movements made by the left and right legs were recorded separately. This was necessary even with symmetric lesions, for ambidextrous locusts were very rare; most insects had a pronounced 'handedness', a preference for response by either the left or right leg. The ganglion consists of linked left and right halves, with limited independence, each controlling primarily its own leg; this was especially obvious in the effects of asymmetric lesions.

(2) Discarded results

Not all individuals tested were included in the results. Locusts were discarded for the following reasons.

(a) Level of responsiveness very low. These were usually moribund animals.
(b) Persistent spontaneous activity of the legs after some lesions.
(c) Spontaneous activity of the flight muscles or thoracic muscles after lesions.
Not many animals fell into any of these groups.

Table 1. *Specimen result of twenty trials after an experimental lesion*

Animal no. E28. Prothoracic ganglion attached only to the
de-afferented mesothoracic ganglion

Excite both legs	Excite left leg
1 RL	11 $\frac{L}{R}LL$
2 R	12 RL
Excite left leg	13 $\frac{L}{R}$
3 $\frac{L}{R}$	14 RL
4 R	15 R
5 RL	Excite left leg
Excite left leg	16 RL
6 R	17 RLRLL
7 RLL	Excite left leg
Excite left leg	18 $\frac{L}{R}L$
8 $\frac{L}{R}$	19 RLR
9 RL	20 L
10 RLR	

$\frac{L}{R}$ indicates that both legs responded and is scored as a first response for both L and R

No. of responses = 20 = 100 % *responsiveness*

Scoring of L/R ratio:
1st L responses = 6;   ·   1st R responses = 19;
2nd L responses = 12;   2nd R responses = 0.
(Multiply first responses by 1, second responses by 0·5, and sum for each side:)
Score L = 12·0;   Score R = 19·0;
Ratio L/R = 12·0/19·0 = 0·63.
L/R ratio less than unity, therefore animal is right-handed.

(3) Scoring of the response

A specimen result of a series of twenty tests on an animal is given in Table 1. The scoring procedure is as follows:

(a) *Percentage response.* All the tests were followed by a response. The responsiveness is therefore 100%.

(b) *L/R ratio.* The 'handedness' of the animal is expressed by the ratio of the score of the left leg to the score of the right leg in a series of tests (*L/R* ratio). The score of the leg is derived as follows: (i) Only the first two leg movements in any response are considered in the result; this is because occasionally an animal will go on responding with one leg up to 20–30 times after a single stimulus, and if all these leg movements are counted the result is badly distorted. (ii) The first leg movement of a response is scored as 1·0, while the second leg movement is scored as only 0·5. To give equal weight to both would distort the result, because a locust which gives equal numbers of left and right leg movements in a series of tests, but invariably uses (say) the right leg first, cannot be considered as ambidextrous. The total score for each leg in the series of twenty tests is obtained in this way, and in the example given in Table 1 they come to: left 12·0, right 19·0. The *L/R* ratio is therefore 0·63. An ambidextrous locust would give a score of unity; the locust of Table 1 is distinctly right-handed. (iii) A difficulty which arises when using ratios is that if a zero score is involved the ratio becomes either zero or infinity, which are unworkable values. To avoid this, an arbitrary score of 1·0 was allotted instead of zero. This slightly reduces the observed differences, but avoids ratios of zero or infinity.

(4) *Comparison of the scores of different animals*

No difficulties arise in comparing the percentage responsiveness of different animals. There is, however, a difficulty in comparing the effects of asymmetric lesions upon handedness, because different individuals start with a different individual bias. In order to make comparison easy it is necessary to obtain a common reference point in all experiments.

Ideally, this reference point would be the natural 'handedness' of the animal determined before the lesions were made to the C.N.S., subsequent changes being expressed relative to this. Unfortunately, the responsiveness of the intact animal is so low that this 'handedness' (*L/R* ratio) cannot be determined. As a substitute the reference *L/R* ratio was taken to be that obtained from the prothoracic ganglion alone, at the end of the lesion series, when it was completely separated from the rest of the C.N.S. and the animal was in consequence highly responsive. This ratio was then equated with unity, and the ratios for other lesions were altered in proportion. The performances of different individuals could then be compared and averaged.

Table 2 gives an example of this process, presenting *L/R* ratios obtained from three different locusts after each had suffered the same series of lesions. The last lesion, lesion 4, results in complete isolation of the prothoracic ganglion, and its ratio is taken as the reference ratio. The previous lesions, being asymmetric, have resulted in the partial disinhibition of the right leg; in these the *L/R* ratio is correspondingly reduced in comparison with the final ratio. Locust E 16 has a reference ratio of 0·77 and is therefore slightly right-handed, E 19 has a reference ratio of 6·0 and is thus markedly left-handed, while E 20 has a reference ratio of 13·3 and is extremely left-handed. As a consequence the effects of the different lesions (first column) are not easily compared between individuals. After dividing through by the reference ratio in

each case, however (last column), it can be seen that the effects of the lesions are similar in all three insects, and serve to disinhibit the right leg, giving a reduction in the L/R ratios.

Table 2. *Specimen result*

L/R ratios for a series of four lesions obtained from three different locusts; (*a*) as first obtained, and (*b*) after division throughout by the basic ratio (lesion 4). Further explanation in text.

Lesion	(*a*) L/R ratio	(*b*) L/R ratio expressed relative to lesion 4
Animal no. E 16		
1	0·075	0·10
2	0·05	0·07
3	0·37	0·48
4 (basic ratio)	0·77	1·0
Animal no. E 19		
1	1·43	0·24
2	1·39	0·23
3	2·31	0·38
4 (basic ratio)	6·0	1·0
Animal no. E 20		
1	1·73	0·13
2	1·52	0·11
3	4·0	0·30
4 (basic ratio)	13·3	1·0

(5) Tests of significance

Although the data presented here are in numerical form, they do not satisfy the requirements of parametric tests of differences between populations, especially when the figures (e.g. the L/R ratio) represent scores rather than frequencies. The randomization test for matched pairs (Siegel, 1956) has been used instead, with two sets of lesions to the same locust providing the matched pair. In the text a statement that a difference exists implies a probability of error of 5 % or less. In the tables the actual probabilities are given.

RESULTS

First series

The head ganglia were disconnected and progressive symmetric lesions were made to the posterior nerve cord. The lesions and their effects are summarised in Table 3. The first lesion to have a significant effect on the responsiveness of the prothoracic ganglion is the cutting of the abdominal/metathoracic connectives, which detaches the whole abdominal chain. Responsiveness was then raised from 7 to 13 %. De-afferentation of the metathoracic ganglion, which would be expected to reduce its activity, caused a further rise in responsiveness to about 30%. Complete removal of the metathoracic ganglion gave 84% disinhibition of the prothoracic ganglion, and further de-afferentation or disconnexion of the mesothoracic ganglion gave only a slight further increase. It would appear that the mesothoracic ganglion by itself exerts little inhibitory influence on the prothoracic ganglion (though of course its activity, and thus its inhibitory effect—see later—may be seriously diminished relative to the normal by the loss of the closely associated metathoracic ganglion), and

almost all the inhibition due to the posterior chain is received either directly or indirectly from the metathoracic ganglion. The L/R ratio did not depart significantly from unity as a result of these symmetric lesions.

Table 3. *Responsiveness of the prothoracic reflex after symmetrical lesions to the posterior nerve cord. Head ganglia disconnected*

Figures are the averages of eight individual performances, each individual being tested twenty times for each lesion

Lesion						
% Response	7	13	31	84	98	98
Probability of difference occurring by chance		0·5 %	0·5 %	0·5 %	2 %	> 95 %
L/R ratio	—	—	—	0·9	1·02	1·0
		(responsiveness too low for determination)				
Probability of difference occurring by chance					> 95 %	> 95 %

Second series (Table 4)

The head ganglia were disconnected and the first lesion disconnected the abdominal chain as before, but the second cut only one of the two meta/mesothoracic connectives. The responsiveness of the prothoracic ganglion rose to 90%, equivalent to total

Table 4. *Responsiveness of the prothoracic reflex after asymmetric lesions to the posterior nerve cord. Head ganglia disconnected*

Figures are averages of seven individual performances, each individual being tested 20 times for each lesion.

Lesion					
% Response	13	96	95	98	98
Probability of difference occurring by chance		1 %	75 %	> 95 %	> 95 %
L/R ratio	—	5·70	7·70	1·72	1·00
	(responsiveness too low for determination)				
Probability of difference occurring by chance			2 %	< 1 %	5 %

removal of the metathoracic ganglion, and further lesions did not give a significant further overall disinhibition. However, the L/R ratio altered from unity to 5·7; that is to say, the disinhibition affected predominantly one side, that on which the lesion had been made. The other, intact side was also partially disinhibited by this operation (though not enough to keep the L/R ratio down) as can be seen in Table 5. The next

Table 5. *Effect of unilateral (left side) section of the meso-/metathoracic connective on responsiveness of the two prothoracic legs. Head ganglia disconnected*

	Responsiveness (no. of acts per 100 trials)	
	Left leg	Right leg
Before section	17·2	18·8
After section	67	36

Figures from nine different locusts, twenty trials each.

lesion made the system still more asymmetric by cutting the meso/prothoracic connective of the same side. Responsiveness remained maximal, but the disconnected side of the prothoracic ganglion became yet more disinhibited relative to the intact side, and the L/R ratio rose further to 7·7. When symmetry was partially restored by cutting the meso/metathoracic connective of the other side, the L/R ratio fell again, but not completely back to unity. From these last two lesions it can be seen that the mesothoracic ganglion has an inhibitory effect, masked in Series 1 but clear with asymmetric lesions. Finally the prothoracic ganglion was completely isolated, and the basic L/R ratio was determined.

Table 6. *Responsiveness of prothoracic reflex after symmetric and asymmetric lesions to the anterior nerve cord. Posterior nerve cord disconnected*

Figures are the averages of nine individual performances, each individual being tested twenty times for each lesion.
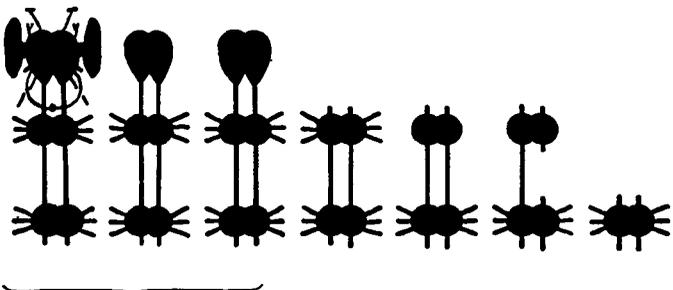
Lesion						
% Response	Not testable (see text)		54	81	90	91
Probability of difference occurring by chance			< 0·2%	15%	75%	
L/R ratio	Not testable (see text)		— (responsiveness too low for determination)	1·06	0·89	1·00
Probability of difference occurring by chance					> 95%	> 95%

Third series (Table 6)

The posterior cord was disconnected and the effects of the head ganglia were tested. When both head ganglia were left intact the prothoracic legs showed almost continuous activity, mainly stepping movements and searching for contact. If the sternal spine sensilla were stimulated in the occasional moment of peace, completely irregular responses occurred, ranging from nothing at all to 3 min. continuous grooming. The attempt to give an accurate description of the results of this lesion was abandoned.

De-afferentation of the brain (cut antennal, optic, tegumentary, labral and frontal nerves) made no change, except to stop the legs being oriented towards objects in the visual field. Nor did unilateral section of the circumoesophageal connective; in particular, the L/R ratio did not seem to be altered by this asymmetric lesion. Bilateral section of the circumoesophageal connectives, on the other hand, left the prothoracic ganglion in a stable testable condition. Responsiveness was 54%; that is, the sub-oesophageal ganglion exerts an inhibitory influence on the prothoracic greater than that of the mesothoracic ganglion alone, but less than that of the combined meso- and metathoracic ganglia. De-afferentation of the suboesophageal ganglion reduced its inhibitory effect, as it did in the case of the metathoracic, and the response level rose to 80%. The L/R could be found at this level of responsiveness and was about unity, as would be expected from a symmetric lesion. Unilateral section of a cervical connective increased the responsiveness up into the final 90–100% level, but had no effect on the L/R ratio, which remained at unity despite the asymmetric lesion. Finally, the prothoracic ganglion was isolated.

Interpretation

The prothoracic ganglion in an intact nerve cord is completely inhibited (see Introduction) and the isolated ganglion is disinhibited. Experiments involving progressive lesions might then lead to two possible conclusions: either (1) inhibition is exerted by a single part of the C.N.S., or (2) summating inhibitory effects are exerted by all parts of the C.N.S. Both these conclusions are partially true. Inhibition is exerted by all parts of the C.N.S. on the prothoracic reflex, but the most important sources are the metathoracic, suboesophageal, and mesothoracic ganglia (in that order). The abdominal chain appears to have little effect. The pronounced effects of the metathoracic and suboesophageal ganglia are greatly reduced if they are de-afferented by cutting their segmental nerves. Thus the inhibitory effect of these ganglia appears to be a function of their general level of activity, and is not constant.

The effects of posterior asymmetric lesions are complex. When the mesothoracic ganglion alone is connected to the prothoracic there is apparently little inhibition. Unilateral disconnexion of the mesothoracic ganglion, however, then produces a unilateral disinhibition, resulting in the alteration of the L/R ratio. How are these two results to be reconciled?

The most plausible hypothesis postulates negative feedback (mutual inhibition) between the two halves of the prothoracic ganglion. There is already some evidence for this in the sequential effect found in testing, and it would be expected on engineering grounds in order to improve the stability of the mechanism. (For example, without

negative feedback there is no reason why the grooming reflex of one leg should not excite a response from the other leg, resulting in oscillation.) If this postulate is accepted then the events taking place as a result of the lesions to the meso/prothoracic connectives would be as shown in Fig. 2. When the mesothoracic ganglion is connected to the prothoracic ganglion inhibitory signals pass along both connectives and inhibit (primarily) their own sides of the prothoracic ganglion. Because of this the inhibition
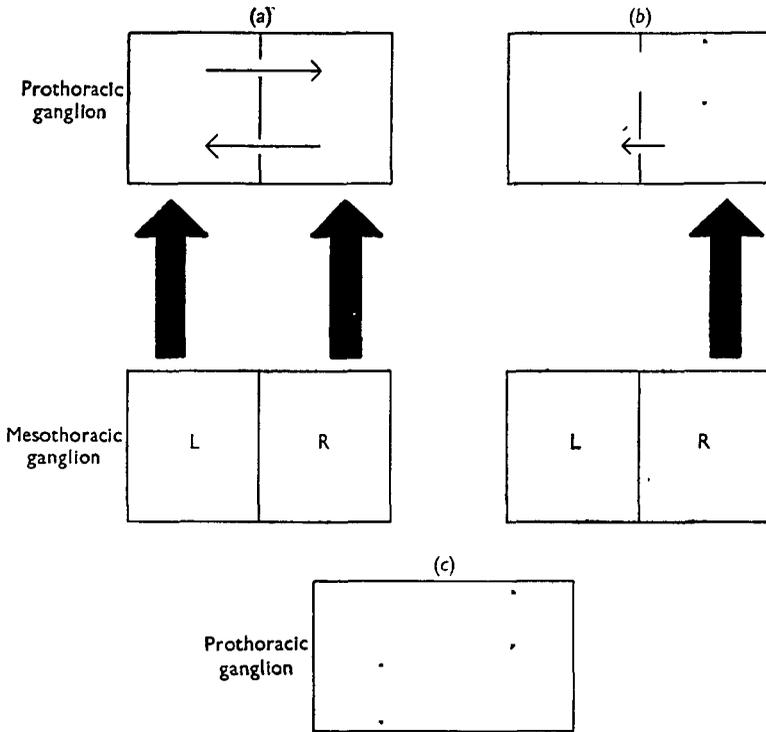

Fig. 2. A model of the inhibitory relationships between the prothoracic and mesothoracic ganglia deduced from the effects of lesions. (a) The state in the intact animal, (b) after cutting the left connective, (c) after cutting both connectives. Further explanation in the text.

exerted by each side of the prothoracic ganglion on the other is small. If one connective is now cut, that side of the prothoracic ganglion is disinhibited. As a consequence its responsiveness relative to the opposite side is increased, and the L/R ratio moves away from unity as observed. As it is disinhibited the inhibitory signal which it sends to the opposite side of its own ganglion is increased, and thus the total inhibition of the intact side is increased and the responsiveness lowered. This further alters the L/R ratio in the same direction. The overall inhibition and thus the responsiveness of the ganglion, however, remain about the same. When both connectives are cut no inhibitory input reaches the prothoracic ganglion from the outside, but as both sides are now disinhibited each exerts a large inhibitory influence on the other. Responsiveness remains unaltered, but as the inhibition is now symmetric once more the L/R ratio returns to unity.

The case of asymmetric disconnexion of the metathoracic ganglion is more complex. This operation produces almost total disinhibition of the prothoracic ganglion and a big alteration in the L/R ratio—clearly the major part of the increase in responsiveness is associated with the unilateral disinhibition of one leg. But the data show that disinhibition is not confined to the side on which the lesion is made; the other side is also disinhibited to a smaller extent (Table 5). A model to fit these observations is shown in Fig. 3. It is assumed for the sake of simplicity that the metathoracic con-
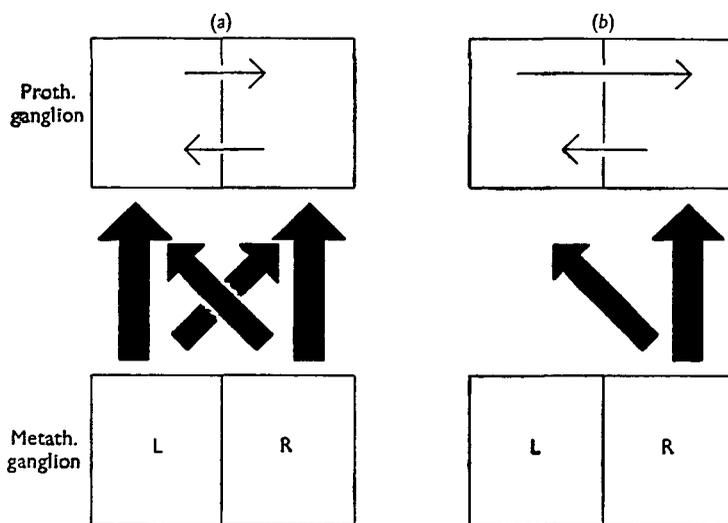

Fig. 3. A model of the inhibitory relationships between the prothoracic and metathoracic ganglia deduced from the effects of lesions. (*a*) The state in the intact animal, (*b*) after cutting the left connectives joining the two ganglia. Further explanation in the text.

nexions pass through the mesothoracic ganglion and influence the prothoracic ganglion directly (see Methods). A more complex model which did not involve this assumption could be built up on the basis of diagrams 2 and 3. Each side of the metathoracic ganglion is known to exert a strong inhibitory influence on the ipsilateral side of the prothoracic, and a weaker one on the contralateral side. These are symbolized in Fig. 3 by arrows of different sizes. When both connectives are intact each side of the prothoracic ganglion receives an inhibitory signal from the ipsilateral side of the metathoracic ganglion, a weaker signal from the contralateral side, and probably a still weaker one from the contralateral side of the prothoracic ganglion (as postulated above). When one connective is cut the intact side of the prothoracic ganglion continues to receive the ipsilateral signal but loses the weaker contralateral one. It is therefore slightly disinhibited. The side which has been disconnected, however, is receiving only the weaker contralateral inhibitory signal from the metathorax, and is therefore largely disinhibited. Negative feedback between the two sides of the prothoracic ganglion will tend to increase this discrepancy between them. The net result is that both sides of the prothoracic ganglion are disinhibited by cutting one connective, but the cut side is disinhibited much more than the other.

If there is negative feedback between the two sides of the prothoracic ganglion, this is probably to be seen in the other ganglia as well. The model diagrams can be

modified to include this assumption, but become too complex for easy appreciation, and the data are not adequate for a mathematical model along these lines. In those models already made there is an assumption of linearity between input and output, but there is no evidence for this—it is merely taken as the simpler alternative. But I suggest that the major features of the two diagrams represent actual physiological relationships.

Early studies on the suboesophageal ganglion suggested an excitory influence on the rest of the nerve cord. This is now doubtful, as the lesions used probably upset the hormonal system regulating activity which is intimately related to the suboesophageal ganglion (Harker (1956), Milburn et. al. (1960)). Recent work (Roeder et al. (1960)) has attributed an inhibitory effect to the nervous connexions between the suboesophageal ganglion and other parts of the nervous system, and this is supported by the present results. Unilateral section of the cervical connectives has no effect on the L/R ratio of the prothoracic ganglion. This means that each side of the suboesophageal ganglion influences both sides of the prothoracic ganglion equally, which is the opposite of what was found for the two posterior thoracic ganglia. Thus the detail of the nervous machinery is different not only from species to species, but also from ganglion to ganglion and almost certainly from reflex to reflex.

DISCUSSION

Most forms of behaviour in animals are in response to stimuli which are continually present at greater or lesser intensity. An animal is almost always to some extent hungry, sexually motivated, frightened, itchy and sleepy. The input to which it actually responds (subjectively the 'strongest') is determined by factors including both the absolute intensity of the stimulus and variation in the physiological state of the animal; the last category includes the results of learning processes as well as more transitory changes. This picture of an animal containing many different action-systems, each already 'ticking over' to some extent, implies inhibitory relations between them if single coherent actions are ever to emerge; it is important not to try to do everything at once.

Such inhibitory relations probably occur at all stages of the systems involved, from sensory input to motor output. Inhibition between effector systems is well known. For instance when a muscle is activated the tonus and stretch reflexes of antagonistic muscles are inhibited. Similarly, there is inhibition between reflexes which involve the same muscle systems. Inhibitory relations involved in the initiation of a response, at the sensory or integrative level, are less well known. Those which have been here described from the integrative level of the locust c.n.s. suggest a generalization for animals as a whole.

The interneuronal system involved in any function of a c.n.s. is linked not only with input and output appropriate to that function, but also to other functional systems with which it may actually share many of its units. Thus, when we consider the nervous machinery responsible for a particular behaviour pattern, this system will also be receiving input from sources other than the ones we are interested in. This information is 'extraneous' to that required by the system to perform the action under consideration. In the locust the probability of obtaining the desired

response (i.e. the grooming reflex) to a standard input is inversely related to the total extraneous signal which arrives simultaneously at the integrating area (the prothoracic ganglion) from other sources. I think this may be an example of a general principle.

Three examples are given below of hypotheses derived from this principle to explain cases of 'attention' and 'distraction'.

(1) A feeding locust requires a stronger electric shock to its antenna to produce a grooming response than a locust which is at rest. I suggest that the input arriving at the brain and prothoracic ganglion as a consequence of feeding (which is non-specific or extraneous as far as the grooming response is concerned) directly inhibits grooming which is also initiated in these areas.

(2) Grooming occurs in animals not only when grooming stimuli are strong, but also immediately before and after rest, in conflict situations, after cold anaesthesia of poikilotherms, during cerebral stimulation, etc. In all these circumstances the other activities of the normal animal which usually inhibit grooming are absent or suppressed. In some birds, e.g. *Sternus* (van Iersel & Bol, 1958) and *Fringilla* (Rowell, 1961 b), the appropriate inhibitory relations have been demonstrated experimentally. I suggest that the input consequent upon the other activities inhibits grooming by a system similar to that found in the locust nerve cord.

(3) It is easier to train, or to elicit a response from, an experimental animal in an environment that is free from other interest, that is, from diverse stimuli. Possibly that part of the brain which responds to these distracting stimuli directly inhibits the system which it is hoped will respond.

It cannot at present be judged whether inhibition of the prothoracic reflex of the locust is proportional only to the quantity of extraneous signal to the ganglion, or whether there are qualitative differences in the effectiveness of this input. The evidence so far suggests the first alternative, that is, that the effect is non-specific. (1) It survives a great many different lesions, which argues against a limited number of special inhibitory tracts. (2) Inhibition can be produced by general electrical stimulation of other parts of the C.N.S. (work in progress). (3) The wide variety of sources of inhibition (at least four different ganglia and also direct sensory input, e.g. tarsal contact). (4) The quantitative rather than qualitative effects of de-afferentation of the inhibitory ganglia suggest that the inhibitory effect is a function of the total input to the ganglion. This input can only be analysed, and correlated with the results given here, by electrophysiological methods; the results of this analysis will be reported elsewhere.

SUMMARY

1. A reflex leg movement mediated by the prothoracic ganglion of *Schistocerca* is completely inhibited under most normal conditions but disinhibited if the ganglion is isolated from the C.N.S.

2. Progressive lesions to the C.N.S. give progressive disinhibition. The main inhibitory areas are the metathoracic, suboesophageal and mesothoracic ganglia.

3. The left and right sides of the thoracic ganglia are to some extent independent in both the transmission and reception of inhibitory signals. There is probably

negative feedback between the reflex systems of the two sides of the prothoracic ganglion.

4. The inhibitory influence of a ganglion on the reflex appears to be proportional to its level of activity and to the amount of signal it is transmitting to the prothoracic ganglion. It is not constant, and is probably not mediated by a limited number of specific inhibitory tracts.

5. The general occurrence of similar mechanisms in animal nervous systems is suggested and discussed.

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