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PROPERTIES OF THE TROCHANTERAL HAIR PLATE AND ITS FUNCTION IN THE CONTROL OF WALKING IN THE COCKROACH

BY R. K. S. WONG* AND K. G. PEARSON
Department of Physiology, University of Alberta, Edmonton, Canada

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SUMMARY

1. The physiological properties of the group of long hair sensilla of the trochanteral hair plate in the cockroach metathoracic leg were studied. The sensilla were divided into type I and type II according to their responses to imposed displacements.

2. Type I hair sensilla responded to dynamic displacements whereas type II hair sensilla responded to both dynamic and static displacements. The hair sensilla are normally excited by phasic flexion movements of the femur near the end of leg protraction.

3. Activity in the trochanteral hair plate afferents had a short latency excitatory effect on the motoneurone producing slow extension movements of the femur and an inhibitory effect on the femur flexor motoneurones.

4. Removal of the trochanteral hair plate in one leg caused overstepping of that leg in a walking animal due to exaggerated flexion of the femur. This change in leg movement can be explained by the removal of the inhibitory influence from the hair plate afferents to the femur flexor motoneurones.

5. We conclude that one function of the trochanteral hair plate is to limit femur flexion during a step cycle.

INTRODUCTION

The legs of the cockroach contain an elaborate system of proprioceptors. These can be divided into five classes, namely the chordotonal organs, the campaniform sensilla, the hair plates, the multipolar stretch receptors and the free nerve endings (Pringle, 1961; Guthrie & Tindall, 1968; Young, 1970). Our knowledge about how these receptors function in the control of walking is very limited. Only the function of the campaniform sensilla in the trochanter has so far been determined (Pearson, 1972; Pearson & Iles, 1973).

Early studies on the hair plate receptors in the proximal part of the cockroach leg led to the suggestion that these receptors are important in the tonic control of leg position (Pringle, 1938, 1961). The extent to which these receptors also function in controlling leg movements during walking is unknown but their involvement in walking must be considered probable since removal of the proximal hair plates in

* Present address: Division of Ophthalmology, Stanford University Medical Center, Stanford, California 94305.

another insect, the stick insect, produced significant changes in the leg movement during walking (Wendler, 1966).

In this paper we report the results of a study designed to determine the function during walking of the hair plate in the trochanter of the cockroach metathoracic leg. The properties of the afferents from this receptor have been re-examined (cf. Pringle, 1938) and their reflex effects on leg motoneurones investigated for the first time. In addition the effect of removal of the hair plate on leg movements in a walking animal has been studied. From this study we concluded that one function of the hair plate is to limit the extent of femur flexion during a step cycle.

MATERIALS AND METHODS

All experiments were carried out on the left metathoracic leg of the adult cockroach *Periplaneta americana* L. The preparation was always kept at room temperature (20 ± 1 °C) when experiments were performed.

To investigate the properties of the trochanteral hair plate and the reflex effect of its afferents on leg motoneurones, preparations in which sensory and motor activity could be recorded upon stimulation of the hair plate were developed. To investigate the function of the hair plate in the control of walking, recordings of the muscle activities were obtained both prior to and after the removal of the hair plate. Changes in the motor output after hair plate removal were examined. The technique of recording muscular activity in a walking animal has been described previously (Pearson, 1972).

(1) *Anatomy of nerve and muscle*

The anatomy of the trochanteral hair plate will be discussed in the results section.

In previous studies, various motor axons in nerve supplying the metathoracic coxal levator and depressor muscles have been identified and labelled according to the amplitudes of the extracellularly recorded action potentials and discharge patterns (Pearson & Bergman, 1969; Pearson & Iles, 1970). Axons 5 and 6 in nerve 6Br4 (notation of Pipa & Cook, 1959) innervate the posterior coxal levator muscle 182 (notation of Carbonell, 1947). Activity in these axons produce slow, graded contractions causing flexion movements of the femur. Axon D_8 in nerve 5r1 innervates the coxal depressor muscles 177 D and 177E. Slow, graded contractions of these muscles produced by activity in axon D_8 cause extension of the femur. Branches of a common inhibitor neurone reach the periphery via both nerve 6Br4 and 5r1. They are labelled 3 and D_3 in eachnerve respectively.

(2) *Stimulation of the trochanteral hair plate*

(*a*) *Mechanical*

The hair sensilla of the trochanteral hair plate were displaced mechanically by a bent insect pin connected to the armature of a vibrator generator (Pye-Ling V47). The vibrator was driven by a Hewlett Packard 3300A function generator. Movements of the insect pin were monitored by a length transducer (Hewlett Packard Model 24DCPT-050). The hair sensilla of the hair plate were made to rest on the bent tip of the insect pin. The hair sensilla were pushed by the insect pin in the direction that they would be deflected during femur flexion. The return of the hair sensilla to their resting position was passive.

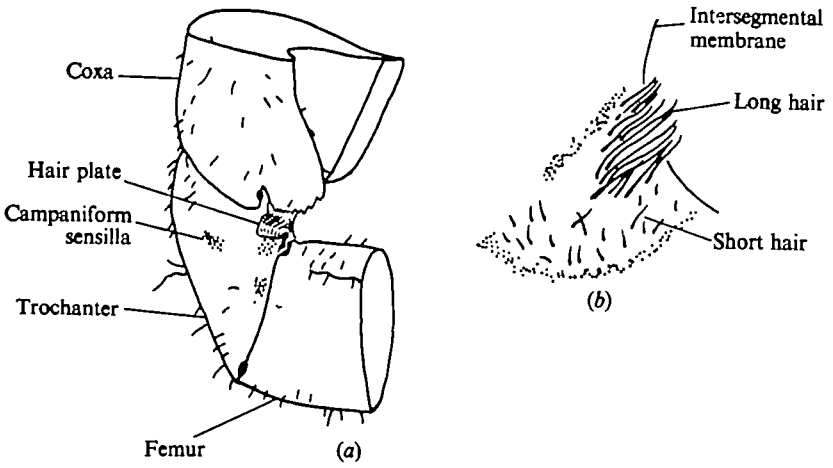

Fig. 1. (*a*) Ventral view of a portion of the left metathoracic leg of the cockroach showing the location of the trochanteral hair plate and three groups of campaniform sensilla in the ventral surface of the trochanter. (*b*) Enlarged view of the trochanteral hair plate. The long hairs resting on the intersegmental membrane of the coxo-trochanteral joint are moved by a fold of the membrane during femur flexion. The small hairs do not contact the intersegmental membrane and they are not displaced by the membrane even during extreme flexion of the femur.

(*b*) *Electrical*

A sharp insect pin was used as an electrode to stimulate the hair sensilla of the hair plate. The pin was gently pressed against the base of the hair sensilla. Positive voltage pulses of 0·05 ms duration 3–30 V were applied for stimulation from a Grass SD5 stimulator. The strength of the stimulus was adjusted so that either activation of single hair plate afferents or simultaneous activation of more than one afferent could be evoked from the hair sensilla.

(3) *Extracellular recording of sensory and motor activity*

All recordings from nerves were made with bipolar electrodes made of 75 μm silver wire. Nerve 5 of the metathoracic ganglion was lifted clear of the haemolymph and coated with petroleum jelly. This allowed recording of the activity in the afferents from the hair plate and the axon of motoneurone D_8 since these axons run in nerve 5. To record the activity in axons 3, 5 and 6 in nerve 6Br4, nerve 6Br4 was cut just distal to the coxal rim near branch 6Br3, and then retracted medially and placed on the recording electrodes.

In order to monitor the activities in axons 5 and 6 and axon D_8 in a walking animal, copper wires of 50 μm diameter, insulated to the tip, were inserted in specific regions of muscles 182C and 177D respectively (Pearson, 1972). The excitatory junctional potentials elicited by axons 5 and 6 and axon D_8 could then be recorded.

RESULTS

(1) *Anatomy of the trochanteral hair plate*

The trochanteral hair plate is formed by a group of 50–60 sensilla and is located close to the ventral coxo-trochanteral condyle (Fig. 1). The hair sensilla rest on the

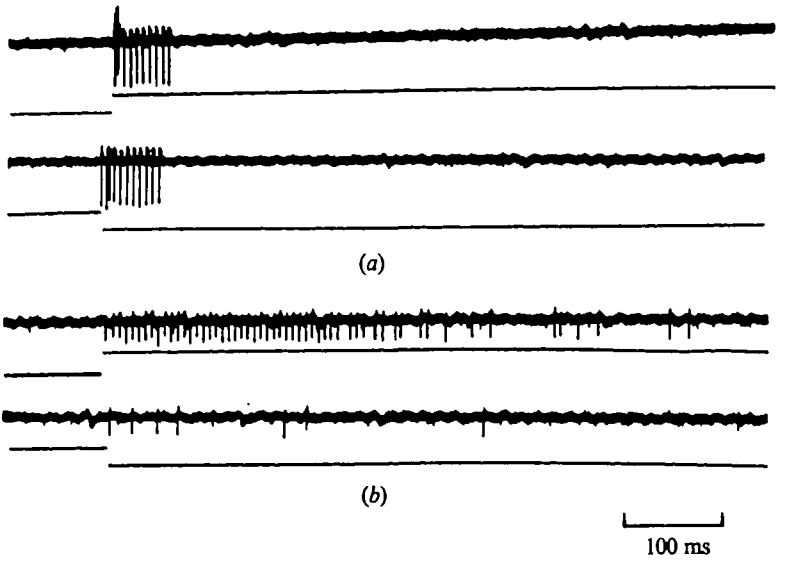

Fig. 2. Response of different hair sensilla to step displacement. Upper trace of each record shows the evoked impulses from the hair sensillum recorded from nerve 5. Lower trace signals displacement of the hair. Upward deflexion signals onset of displacement when the hair is pushed away from the intersegmental membrane. Downward deflexion signals release of displacement when the hair returns to its original resting position by its own elasticity. (*a*) Type I sensilla. Notice the intense initial phasic component evoked by the onset of displacement which is absent during the release. (*b*) Type II sensilla. The response to the onset of the displacement adapted more slowly than the same response of type I sensilla. The response to the release of the displacement is less intense than the response to the onset.

intersegmental membrane of the coxo-trochanteral joint and are displaced by a fold of the membrane during femur flexion. The axons from the hair sensilla run in nerve 5r5b. Nerve 5r5b joins nerve 5 in the trochanter near the coxo-trochanteral joint (Nijenhuis & Dresden, 1955).

The hair sensilla of the hair plate could be divided into two groups according to their relationship with the intersegmental membrane of the coxal trochanteral joint (Fig. 1). About 30 sensilla, from 30 to 70 μm in length, rested on the intersegmental membrane. Individual sensillum of this group showed a curvature that enabled it to rest along its length on the fold of the intersegmental membrane. Another group of sensilla, located more distal to the joint, did not contact the intersegmental membrane. The length of the sensilla of this group ranged from 5 to 30 μm. Observations under the dissecting microscope revealed that they were not displaced by the intersegmental membrane even during extreme flexion of the femur. All the results in our present study were obtained from the group of longer hairs that contacted the intersegmental membrane. These sensilla were arranged in rows such that a folding of the intersegmental membrane would first displace the most proximal row of sensilla. With further flexion of the femur the increased folding of the membrane would displace the next row of sensilla and so on. Thus the arrangement of the hair sensilla is such that increased numbers of sensilla are displaced when the flexion of the femur is increased.

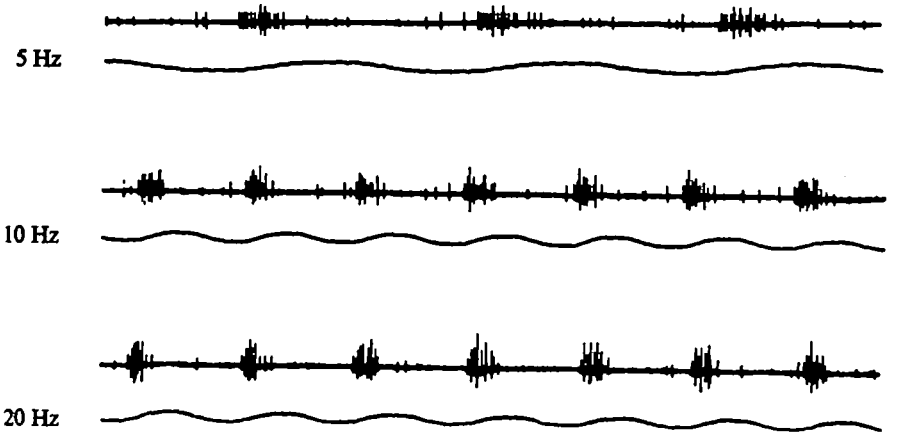

Fig. 3. Response of the whole group of long hairs to sinusoidal displacement. The upper trace of each record shows the evoked activity from the hair sensilla recorded by electrodes placed on nerve 5. The lower trace of each record signals the displacement of the hairs. An upward direction shows that the hairs are pushed away from the intersegmental membrane. When the stimulating frequency is at 5 Hz, the impulses with the greatest amplitude recorded from nerve 5 are generated by type I sensilla. Notice that the maximum response always occurs before the maximum displacement.

(2) *Properties of the trochanteral hair plate*

(*a*) *Mechanical stimulation*

Individual hair sensilla were separated out from the group and stimulated mechanically. Impulses elicited from different hair sensilla recorded by electrodes placed on nerve 5 varied in amplitude. It was observed that recorded impulses with the largest amplitude were always elicited from the longest hair sensilla. When step displacements were applied to the hair sensilla, the onset of the step displacement pushed the sensilla away from the intersegmental membrane. This direction of displacement was the same as that along which the sensilla would be displaced during femur flexion. During the release of the step displacement, the hair sensilla returned to their initial position. The group of long hair sensilla normally resting on the intersegmental membrane can be divided into two types according to their response to the mechanical displacement. These two types are named type I and type II hair sensilla. Type I hair sensilla responded to the onset of the step displacement with an initial phasic discharge followed by a quick and complete adaptation (Fig. 2*a*). The size of the impulses generated by type I hair sensilla recorded by a pair of bipolar electrodes placed on nerve 5 was in the range of 0·5–2·0 mV. For type II hair sensilla, the adaptation of the response to the onset of a step displacement was slower and only complete for small displacements (Fig. 2*b*). For larger displacements the type II sensilla tonically discharged during a maintained displacement. The magnitude of this static discharge was monotonically related to the degree of displacement. The size of the impulses generated by the type II hair sensilla recorded extracellularly was always smaller than 0·5 mV. Both type I and type II hair sensilla showed directional sensitivity. For the type I sensilla, the intense initial phasic discharge accompanying the onset of the displacement was not present during the release. For type II sensilla, the onset of the displacement was accompanied by a more intense discharge than the release of the displacement.

The response of the hair sensilla to sinusoidal displacement was examined. A large number of hair sensilla, both type I and type II sensilla included, were made to rest on the stimulating insect pin and the summed discharge evoked from the hair sensilla was recorded. Fig. 3 shows that the sensilla responded phasically to the imposed displacement. The response showed directional sensitivity. For stimulating frequencies of 20 Hz and less, discharges were elicited from the sensilla only when they were pushed away from the intersegmental membrane. For higher frequencies the sensilla was also activated during the return movement to the resting position, but this activity was considerably less intense than that occurring during movements away from the resting position. Within each cycle of displacement, the most intense discharge was always elicited during the maximum velocity portion of the cycle. For low frequencies of displacement (under 10 Hz) type I sensilla responded to a much smaller portion of the cycle than type II sensilla. As the frequency of displacement increased, the summed discharge frequency of both type I and type II sensilla within each cycle increased. In addition, type I sensilla were recruited to respond earlier in the cycle, although they still responded to a smaller portion of the cycle than type II sensilla. The dynamic responses of the two types of sensilla to periodic and random displacements have been studied quantitatively and will be described in more detail (French & Wong, 1975).

(b) Response to electrical stimulation

The strength of the electrical shocks applied to the base of the hair sensilla could be adjusted so that single afferents from the hair plate were activated by each shock. Responses were considered to be elicited from a single hair sensillum if they displayed the all-or-none characteristics at threshold stimulus strength. The size of the impulse for single afferents recorded on nerve 5 by a pair of bipolar electrodes ranged from 0·2–2·0 mV. Increasing the stimulus strength at any one of the sites of stimulation resulted in the activation of a number of hair sensilla and the recording of a synchronized afferent volley by electrodes placed on nerve 5. For synchronized responses elicited from several hair sensilla, decreasing the stimulus strength by a sufficient amount resulted in a sudden decrement of the amplitude of the afferent volley. Thus the occurrence of a single unit response and a synchronized response could be readily distinguished.

The conduction velocity for impulses elicited from different hair sensilla was determined by placing two pairs of bipolar electrodes of a known distance apart on nerve 5. The time that elapsed between the recording of the evoked impulse by one pair of electrodes and the next was measured. The conduction velocity could then be calculated. The conduction velocity of the afferents from different sensilla ranged from 3·5–5 $m.s^{-1}$. The relationship between the conduction velocity and the amplitude of the extracellularly recorded impulses elicited from the hair sensilla has been systematically investigated. It was found that the relation between the log amplitude of the impulse and the log of its velocity of propagation is linear with a slope of 0·4. The amplitude of the extracellularly recorded impulse, then, is proportional to the 0·4th power of the conduction velocity. This relationship between the amplitude of the extracellularly recorded impulse and its conduction velocity is the same as that obtained for the motor axons in the cockroach (Pearson, Stein & Malhotra, 1970).

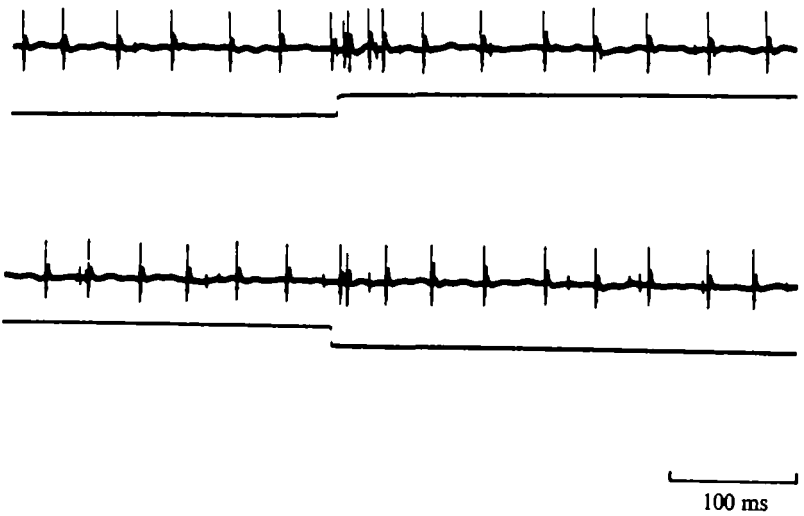

Fig. 4. Response of motoneurone D_s to step displacement of the hair sensilla. Upper trace motoneurone D_s activity recorded by electrodes placed in muscle 177D. Motoneurone D_s is spontaneously active. Lower trace signals the displacement of the group of long hair sensilla. Upward deflexion signals onset of displacement and downward deflexion signals release of displacement.

(3) *Reflex effects of the hair plate on slow depressor motoneurone* D_8

(*a*) *Response to mechanical stimulation*

The onset of a step displacement of the hair sensilla of the hair plate transiently increased the spontaneous activity of motoneurone D_8 (Fig. 4). This response in motoneurone D_8 adapted quickly although the displacement of the hairs was maintained. The release of the displacement was accompanied by a much weaker excitation of motoneurone D_8. It has been shown that the hair sensilla respond with a more intense discharge during the onset of the step displacement than during the release (Fig. 2). This property of the hair sensilla can account for the much stronger reflex response of motoneurone D_8 during the onset of the step displacement of the hair sensilla.

Fig. 5 shows the reflex response of motoneurone D_8 during sinusoidal displacement of the hair sensilla of the hair plate. Motoneurone D_8 was reflexly activated only when the hairs were pushed away from the intersegmental membrane. The return of the hair sensilla to the resting position did not activate any motoneuronal response. During low frequencies of displacement, the reflex response of motoneurone D_8 was superimposed on its spontaneous activity. Above 15 Hz, the spontaneous activity of the motoneurone was suppressed and the reflex response of motoneurone D_8 could be elicited in a 1:1 manner up to 90 Hz. However, at this high frequency of hair sensilla displacement, the reflex response adapted after the initial one or two seconds. At frequencies of displacement lower than 50 Hz, the reflex response could be elicited for tens of seconds without showing adaptation.

(*b*) *Response to electrical stimulation*

In order to study the latency of the reflex response of motoneurone D_8, electrical stimulation was used to excite the afferents from the hair plate. Simultaneous

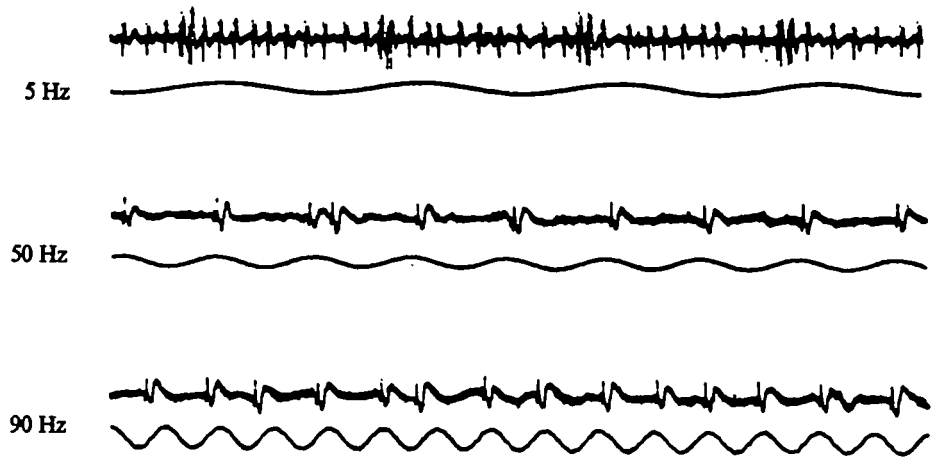

Fig. 5. Response of motoneurone D_s to sinusoidal displacement of the hair sensilla. Upper trace motoneurone D_s activity recorded by electrodes placed in muscle 177D. Notice the shape of the recorded potential at 50 and 90 Hz of hair displacement. The initial spike is caused by the impulse propagating in axon D_s and the longer diphasic (negative–positive) potential is caused by the muscle potential evoked in muscle 177D by the nerve impulse (positive direction upwards). Lower trace of each record signals the displacement of the hairs. Upward direction signals that the hairs are pushed away from the intersegmental membrane. Note the 1:1 following of the motor response when the displacement frequency is as high as 90 Hz.

stimulation of a number of afferents excited motoneurone D_s after a short latency. Fig. 6 shows a record of the synchronized sensory volley and the motoneurone D_s impulse response recorded by a pair of bipolar electrodes placed on nerve 5. It can be observed that the sensory volley and motoneurone impulse are opposite in the order of their positive and negative phases. This feature of the recorded extracellular activity enabled us to differentiate between sensory volleys and motoneurone impulses travelling in the opposite direction in a mixed nerve (Stein & Pearson, 1971). In addition, the motoneurone D_s impulse recorded on nerve 5 was identified by a 1:1 correspondence with the junctional potential recorded from muscle 177D.

An impulse elicited from a single sensillum of the hair plate produced an excitatory effect on the activity of motoneurone D_s. This effect was seen for both type I and type II sensilla (recognized by size of extracellularly recorded impulse). Thus both types of sensilla established excitatory connexion with motoneurone D_s. Fig. 7*a* shows the distribution of latencies of the impulse in motoneurone D_s following an impulse elicited in a single hair sensillum. There was considerable variation in the latency of the response. The variability in latency was reduced when the stimulus strength was increased to elicit a synchronized volley from several hair sensilla (Fig. 7*b*). The minimum latency of the motoneurone response, however, was not affected by the changes in strength of the afferent input. Following the synchronized sensory volley, the motoneuronal response was evoked after a short delay. Fig. 7(*b*) shows that the occurrence of the motoneuronal response tends to peak with a delay of 2·2 ms following the sensory volley. This value of delay was taken as the minimum reflex delay measured at the point of recording on nerve 5. Any motoneurone impulses occurring sooner than 2·2 ms following the sensory volley were most probably generated spontaneously and were not considered to be reflex responses.

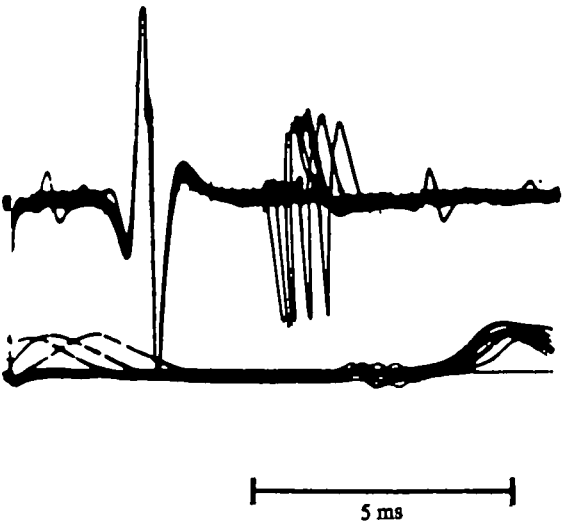

Fig. 6. Records show the electrically evoked synchronized afferent volley from the hair plate sensilla and the response of motoneurone D_s. Notice that the sensory volley and the motoneurone impulse are opposite in the order of their positive and negative phases. Lower trace is the recording in muscle 177D. Each efferent impulse always generates a muscle potential in muscle 177D, showing that the efferent impulse is evoked in motoneurone D_s.

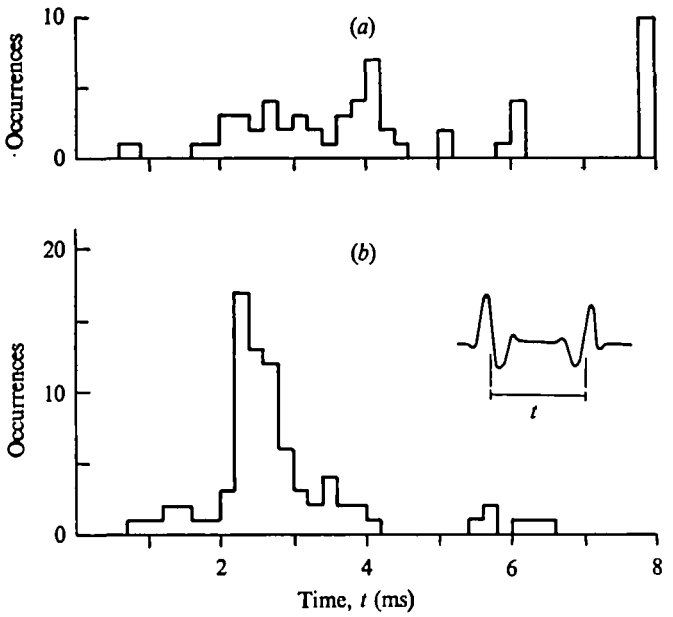

Fig. 7. Histogram of the latency of the spike evoked in axon D_s by afferent activity of the hair plate. Points on the recorded afferent volley and efferent impulse taken for the measurement of latency are shown in the inset. (*a*) Latency of motoneurone D_s response following the activation of a single hair sensillum. The number of responses occurring later than 8 ms following the afferent impulse is shown in the last column. (*b*) Latency of motoneurone D_s response following simultaneous activation of a number of hair sensilla. Motoneurone D_s is spontaneously active; impulses occurring sooner than 2·2 ms following the afferent input are most probably generated spontaneously and are not considered to be reflex responses (see text).

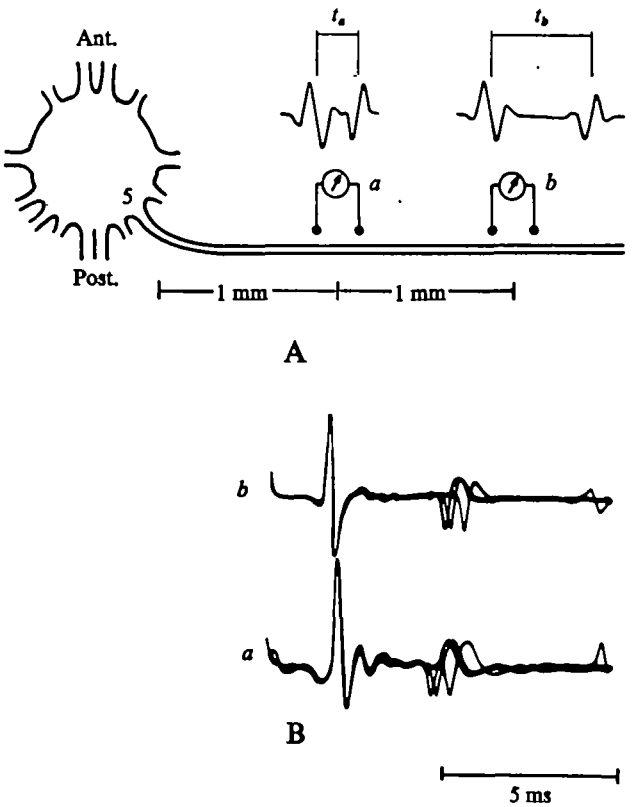

Fig. 8. (A) Diagram showing the arrangement of electrodes for the measurement of central latency. The reflex latencies recorded by electrode pair (*a*) and pair (*b*) are t_a and t_b respectively. $t_b - t_a$ = time for afferent and efferent activity to propagate 1 mm. Therefore central latency = $t_a - (t_b - t_a)$ ms. (B) Upper trace: record of afferent and efferent activity recorded by electrode pair *b*. Lower trace: afferent and efferent activity recorded by electrode pair *a*.

To measure the minimum central latency of the reflex, two pairs of bipolar electrodes were placed on nerve 5. The proximal pair of electrodes was placed at a distance of 1 mm from the root of nerve 5, and the distal pair of electrodes was placed at a distance of 1 mm from the proximal pair (Fig. 8A). A synchronized sensory volley was then evoked to activate motoneurone D_8. Fig. 8B shows the sensory volley and the motor impulse recorded with the electrode arrangement illustrated in Fig. 8A. The difference in the reflex latencies recorded at the distal and proximal pairs of electrodes gives the sum of the time required for sensory volley and motoneurone D_8 spike to propagate 1 mm. By subtracting this sum from the reflex latency recorded by the proximal pair of electrodes, the central delay can be obtained (see legend of Fig. 8). From five preparations, the minimum central delay was calculated to be 1·3 ms. Thus with this electrode arrangement, the central delay can be calculated without having first to compute the propagation velocity of the sensory volley and motor spike.

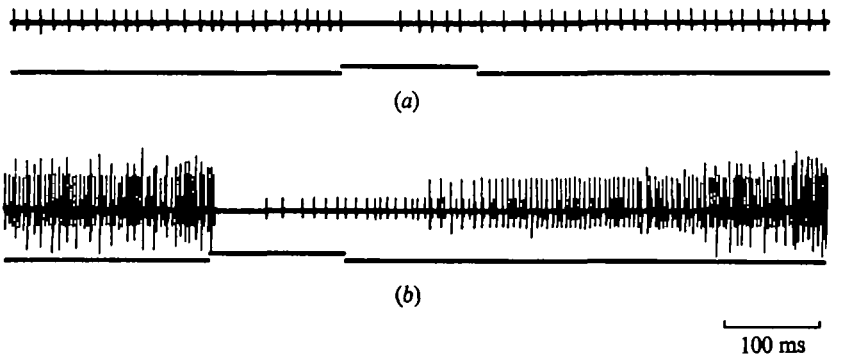

Fig. 9. Record showing inhibition of tonic activity of flexor motoneurones 5 and 6 and common inhibitor neurone 3 by a displacement of the hairs of the hair plate. (*a*) Inhibition of activity in motor axon 3 alone. (*b*) Inhibition of activity in motor axons 3, 5 and 6 during a period of intense flexor activity. Top trace shows the activity of motor axons 3, 5 and 6 recorded from nerve 6Br4. The impulse with the smallest recorded amplitude is generated in motor axon 3. The impulse with the largest recorded amplitude is generated in motor axon 6. The lower trace of the record signals the displacement of the hairs. An upward deflexion indicates that the hairs are pushed away from the intersegmental membrane and a downward deflexion indicates the return of the hairs to the resting position.

(4) *Reflex effect of the trochanteral hair plate on flexor motoneurones and common inhibitor neurone*

Onset of the step displacement of the hair sensilla produced a transient inhibition of the tonic activity of flexor motor axons 5, 6 and the common inhibitor axon 3 (Fig. 9). It was observed that the duration of inhibition of the neurones was directly related to their size. Thus the activity of axon 3, the axon of the smallest neurone, was inhibited for the shortest period of time. The duration of inhibition for axon 6, the largest axon that was active before the displacement of the hair sensilla, was the longest. Single afferents, excited by electrical stimulation of the hair sensilla of the hair plate, did not produce any observable inhibition of the activity of axons 3, 5 and 6. Synchronized volleys from several hair sensilla had to be evoked before the activity of axons 3, 5 and 6 could be inhibited. An estimate of the latency of inhibition was obtained by measuring the time elapsed from the onset of the step displacement to the suppression of the tonic activity. The latency obtained was less than 10 ms.

Rhythmic bursting activity of axons 3, 5 and 6 generates the flexion movement of the femur during walking. Previous study has shown that these rhythmic bursts can be generated in deafferented preparations (Pearson & Iles, 1970). We have found that stimulation of the hair plate with high frequency shocks (100 Hz) influenced the timing of these rhythmic bursts. Preparations with cut thoracic connectives were used for this study since rhythmic bursts of axons 3, 5 and 6 could be elicited more easily. Fig. 10(*a*) shows that when the hair sensilla of the hair plate were stimulated between the flexor bursts, there was a suppression of the burst activity. Burst activity then resumed after a delay following the cessation of the stimulus to the hair sensilla. The occurrence of the first burst following the stimulus was not usually at the instant when a burst of activity would have been expected had the hair sensilla not been stimulated. In other words, the rhythm of the flexor burst was reset by the afferent activities from the hair plate. In other instances when the hair sensilla were stimulated

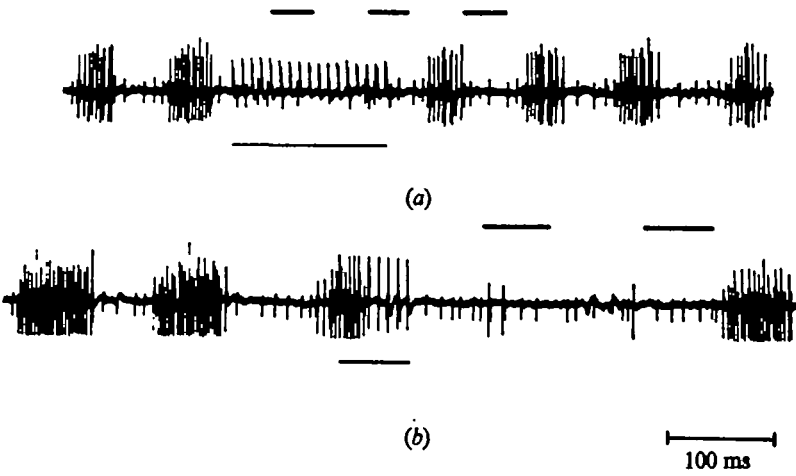

Fig. 10. Records of inhibition of rhythmic flexor burst by repetitive electrical stimulation of the hair sensilla of the hair plate. Activity of axons 3, 5 and 6 is recorded by electrodes placed under nerve 6Br4. The application of electrical shocks is indicated by the line drawn under the nerve record. The stimulus artifact generated by the shock can be observed. The bars above the nerve record indicate where the flexor bursts would have occurred had the stimulus not been applied. (*a*) The electrical shocks were applied between the flexor bursts. (*b*) The electrical shocks were applied during the flexor burst.

during a flexor burst, there was a shortening of the flexor burst in addition to the inhibition of the next flexor burst (Fig. 10*b*).

(5) *Effect of removal of the hair plate on the activity of the flexor motoneurones 5 and 6 and the extensor motoneurone* D_8

The hair plate can be easily removed by a pair of forceps with minimum damage to the surrounding curicle. Subsequent to removal, flexion of the operated leg was exaggerated during walking. This overstepping effect caused the operated metathoracic leg to collide with the ipsilateral mesothoracic leg during flexion. The same effect on leg movement (overstepping) has been described by Wendler (1966) when the coxal and trochanteral hair plates were removed in the stick insect.

Recording of muscular activities in an operated animal enabled us to examine the changes in motor output which were associated with the abnormal leg movements following hair plate removal. An analysis of results in two animals revealed that (1) the durations of the flexor bursts in the operated leg were prolonged compared to those in the normal leg (Fig. 11*a*), (2) the intensity of the flexor burst was increased (Fig. 11*b*), and (3) the initiation of the extensor burst following the end of the flexor burst in a step cycle in the operated leg was not delayed.

DISCUSSION

(1) *Properties of trochanteral hair plate*

The group of long hair sensilla of the hair plate can be divided into two types according to their responses to imposed displacements. Type I sensilla responded transiently to step displacements. The adaptation of the response was complete. The response of type II sensilla to a step displacement adapted more slowly and the

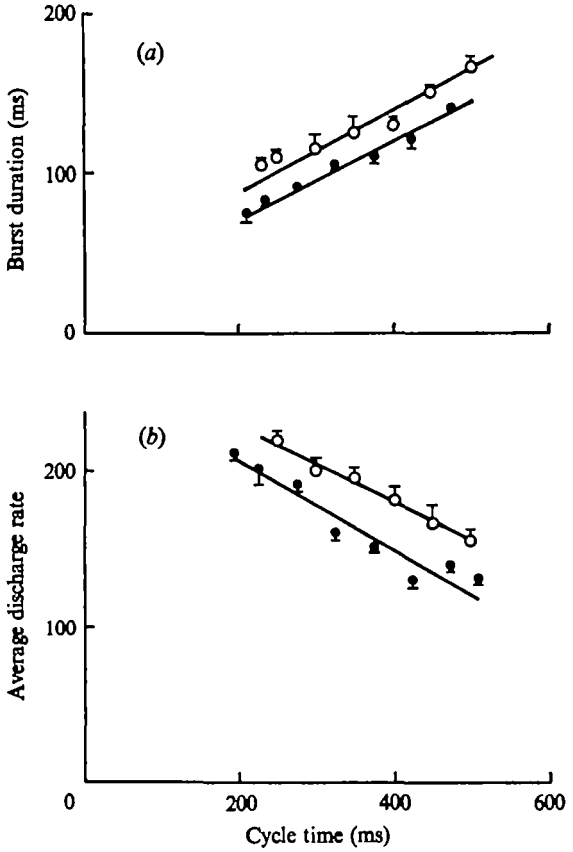

Fig. 11. Graphs showing the effect of removal of trochanteral hair plate in one leg on the burst duration and average discharge rate of the flexor burst in the operated leg during walking. ○, Plot of the record obtained after hair plate removal. ●, Plot of records obtained before hair plate removal. The bars above and below the circles indicate the standard deviation. (*a*) Graph of burst duration versus cycle time. (*b*) Graph of average discharge rate versus cycle time.

adaptation was complete only for small displacements. With sinusoidal displacement of a large number of hair sensilla, the activity of the afferents of the hair sensilla (both type I and type II) is most intense at the maximum velocity portion of the stimulus cycle (Fig. 3) provided that the stimulus frequency was within the range of 1–20 Hz (which is the frequency range for leg movements in a walking cockroach). As the stimulus frequency increases, the discharge frequency of the hair sensilla afferents within a stimulus cycle also increases. These observations suggest that the hair sensilla, both type I and type II, signal the velocity of the imposed displacement. More detailed analysis of the responses of the hair sensilla with sinusoidal and random displacements revealed that type I sensilla respond to the velocity of displacements whereas type II sensilla respond to both the position and velocity of displacements (French & Wong, 1975). The response of the sensilla to sinusoidal displacement also shows directional sensitivity. For frequencies of 20 Hz and less responses are only elicited from the hair sensilla when the direction of imposed displacement is the same as that along which the hair sensilla will be displaced by the intersegmental

membrane during femur flexion. Thus we conclude that the hair sensilla are excited by flexion movements of the femur in a walking animal.

The anatomical arrangement of the hair sensilla is such that they are not displaced by the intersegmental membrane until the femur is in a relatively flexed position. Furthermore, the hair sensilla are arranged in rows such that increased flexions of the femur will displace a larger number of hair sensilla. The hair sensilla will therefore only be excited by movements of the femur near the end of the protraction phase of leg movement in a walking animal. Hence the input from the hair plate will provide information about the position of the femur near the end of the protraction phase.

The results on type II sensilla showing that tonic discharges are evoked by higher levels of displacement suggest that the hair plate might have a role in controlling the static position of the femur, provided that the type II sensilla are displaced to such an extent that tonic discharge can occur. We have not systematically examined the discharge rate of the trochanteral hair plate at various coxo-trochanteral angles. However, it is clear that when the femur is at an extended position, no tonic discharge can be recorded from the hair plate. Hence, if the hair plate has a role in the control of posture, it will not be effective when the femur is in an extended position.

Until now the trochanteral hair plate has been considered to be important only in registering *static* position of the femur (Pringle, 1938, 1961). This suggestion was based on the observation that sensory discharge from the hair plate afferents was incompletely adapting. Our finding that the hair plate sensilla respond mainly to velocity means that this view must now be modified. The primary function of the hair plate appears to be to signal the position of the femur near the end of leg protraction in a walking animal. For the generation of this signal a *phasic* flexion movement of the femur is required. The reason for the difference between our conclusion and Pringle's is not clear. It should be mentioned that in Pringle's study, emphasis was placed on investigating the properties of the inner coxal hair plate although it was commented that the properties of the trochanteral hair plate were the same as those of the inner coxal hair plate. Furthermore, it is possible that in Pringle's study, only type II sensilla were selectively stimulated with high levels of displacement, hence tonic discharges were recorded from the afferents of the sensilla.

(2) *Reflex effect of the trochanteral hair plate afferents onto the femur extensor and flexor motoneurones*

The afferent activity of the hair plate reflexly excites the femur extensor motoneurone D_8 and inhibits the flexor motoneurones 5 and 6. The excitatory connexion with motoneurone D_8 can follow high frequencies of afferent input, and the minimum central latency of the reflex is short (1·3 ms). The time for this latency includes (1) sensory conduction time within the ganglion, (2) synaptic delay, (3) time for the rise of EPSP to threshold, and (4) motor conduction time within the ganglion. Assuming that the synaptic site was 200 μm from the root of nerve 5 and the average motor and sensory conduction time was 4 m.s^{-1}, then (1) plus (4) amount to 0·1 ms. Assuming that the rise of EPSP to threshold requires 0·5 ms, an estimate of the synaptic delay will be 0·7 ms. This short synaptic delay and the high 1:1 following frequency of the reflex motor response suggest that the excitatory connection is monosynaptic. In the following paper (Pearson, Wong & Fourtner, 1976) we confirm that this is so.

The inhibitory effects of the afferent activity from the hair plate affect both the tonic and bursting activity of the flexor motoneurones (Figs. 9 and 10). During rhythmic bursting activity of flexor motoneurones input from the hair plate can reset the rhythm of the bursts (Fig. 10). Previous studies have shown that the flexor bursts are generated by a system of non-spiking interneurones (Pearson & Fourtner, 1975), and in the next paper we show that the hair plate afferents excite and inhibit a number of non-spiking interneurones (Pearson, Wong & Fourtner, 1976). These results suggest that the afferent activity of the hair plate has direct influence on the system of interneurones producing the flexor bursts. The inhibitory effect of the hair plate afferent on the tonic activity of the flexor motoneurones 5 and 6 is of short latency. An approximate estimate of the latency inhibitory pathway was less than 10 ms. This inhibitory effect is probably mediated via a disynaptic pathway (Pearson, Wong & Fourtner, 1976).

(3) *Function of the trochanteral hair plate during walking*

Following the removal of the trochanteral hair plate in the leg of the cockroach, the operated leg oversteps during walking due to exaggerated flexion movement of the femur. Correspondingly, the activity of the flexor bursts is more intense and the duration of the bursts is prolonged. These changes in motor activity of the flexor burst can be a direct consequence of the removal of the inhibitory effect of the hair plate afferents on the flexor motoneurones and/or the system of interneurones producing the flexor bursts. In a normal animal, femur flexion presumably excites the hair plate afferents near the end of protraction and this afferent activity reduces the intensity and duration of the flexor burst during every cycle of walking. The fact that the animal oversteps following the removal of the hair plate suggests that the system of interneurones producing the flexor burst always generates a flexor burst with prolonged duration and sensory feedback is required to terminate the flexor burst in every cycle of walking. A similar function of the phasic sensory feedback is described in the masticatory system of the snail. During feeding activity, the input from mechanoreceptors inhibits the activity of the protractor motoneurones which otherwise might continue to fire into the retraction phase (Kater & Rowell, 1973). In the locust flight system, inputs from the wing stretch receptors excited during wing elevation inhibit the elevator motoneurones and excite the depressor motoneurones. These reflex pathways may therefore function to limit the amplitude of wing elevation (Burrows, 1975). It is perhaps significant that in all these motor systems (walking, mastication and flight) reflexes function to terminate the motor activity underlying the phase of movement in which there is unlikely to be any variation in load. A similar control for the position of end flexion in the forelimb of the dog has also been described (Orlovsky & Shik, 1965). It was found that during walking, the elbow of the dog always flexed to a definite angle irrespectively of the initial angle when flexion began.

The advantages of utilizing the feedback from the hair plate afferents to terminate the centrally generated flexor burst are not immediately apparent. Possibly it is involved in preventing a decrease in amplitude of femur flexion with muscle fatigue. Without inhibitory feedback from the hair plate to the flexor motoneurones and/or the flexor burst generating system any fatigue in the flexor muscles would reduce the

amplitude of the flexion movement. However, if the hair plate functions to terminate the centrally generated flexor burst and is activated at a fixed angle of flexion of the femur (see section I of the Discussion), then the amplitude of the femur movement will remain constant even with fatigue of the flexor muscles. Another possible function of the negative feedback from the hair plate to the flexor motoneurones in the hind and middle legs is to prevent mechanical interference of these legs with the adjacent anterior leg during walking.

Since the hair sensilla of the hair plate are activated near the end of the protraction phase of leg movement in a walking animal, the excitatory connexion of the afferents of the hair plate on the extensor motoneurone D_8 could be important in the initiation of the extensor burst. Accordingly it can be assumed that if the hair plate is removed, the occurrence of the extensor burst in a cycle will be delayed, causing a longer interval between the end of a flexor burst and the start of an extensor burst. However, this expected result was not observed. Probably other afferent channels (e.g. input from campaniform sensilla) are involved in initiating the extensor burst and the removal of one channel may not produce significant changes. Therefore the function of the hair plate in initiating the extensor burst during walking cannot be excluded by our negative finding. The excitatory pathway from the hair plate to the extensor motoneurone D_8 may also function to stabilize leg posture during standing. Any external disturbance which tends to flex the femur will excite the hair plate and hence reflexly increase the level of activity in the femur extensor motoneurone D_8. Consequently an extension force will be developed to resist the imposed flexion.

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