HINDLEG TARGETING DURING SCRATCHING IN THE LOCUST

T. MATHESON*

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

Summary

Intact locusts (*Schistocerca gregaria*) respond to tactile stimulation of their folded wings with rhythmic scratching movements of the ipsilateral hindleg that are directed towards the site of stimulation. For example, sites near the base of a wing elicit anteriorly directed scratches, whereas sites near the distal end of a wing elicit posteriorly directed scratches.

Locusts also scratch in response to tactile stimulation of a wing that is held outstretched in a posture similar to that normally adopted during flight, but they fail to alter their leg targeting to compensate for this changed position of the stimulus site. Instead, they scratch at an empty point in space near the abdomen, where the stimulus site would have been if the wing was folded in the resting posture. This inappropriate scratching does not result from mechanical constraints on the hindleg's movement, from stimulation of abdominal sensory receptors, or from an absence of sensory information from the outstretched wing. It also persists when the metathoracic ganglion that controls movements of the hindlegs is isolated from the remainder of the central nervous system (CNS).

Targeted scratching of sites on the wings of locusts therefore appears to be fixed relative to body coordinates and does not take into account alterations of the target wing's position.

Key words: locust, *Schistocerca gregaria*, scratch reflex, leg targeting, proprioceptive feedback.

Introduction

The investigation of rhythmic scratching movements made in response to stimulation of discrete regions of the body surface of an animal provides insights into the mechanisms underlying targeting of limb movements. For targeting to be successful, an animal must translate a set of spatial coordinates derived from exteroceptive sensory inputs that represent the target site into a coordinated temporal activation of motor neurones to drive the scratching limb towards the appropriate point in space. If the stimulus site is on another limb, the animal may also need proprioceptive information from that limb to enable scratch targeting to compensate for movements of the stimulus site relative to the body. The animal may also make use of proprioceptive sensory information encoding the position of the scratching leg.

Sherrington (1906, 1910) demonstrated that tactile or chemical stimulation of different regions of the body surface of cats and dogs can elicit rhythmic directed scratching movements of a hindleg, with a form and frequency different to locomotory movements. The area of skin that can be stimulated to elicit a scratch is termed the receptive field of the reflex (Sherrington, 1906) and, in the dog, different points of stimulation within that receptive field have different efficacies in producing the movement. Moreover, the form of the movement differs slightly depending on the particular site of stimulation so, for example, the dog's hindleg is moved further anterior to target anterior points of stimulation.

The scratch reflexes of the frog and turtle, but not the cat, have several forms, depending on the site of stimulation (reviewed by Stein, 1983). In the turtle, three distinct reflexes (the rostral, caudal and pocket scratches) can be distinguished by the part of the leg used to rub against the target site (Mortin *et al.* 1985), and by characteristic patterns of muscle activation (Robertson *et al.* 1985). These motor patterns can be elicited even when the animal is immobilised using a neuromuscular blockade. In a decerebrate cat treated with curare so as to prevent muscle activation, tactile stimulation produces patterns of motor activity similar to those recorded during normal scratching (Deliagina *et al.* 1975), but this fictive activity only occurs if the scratching leg is held in an approximately normal scratching posture, and stops if the leg is deflected backwards (Berkinblit *et al.* 1978). Similarly, proprioceptive information from the scratching leg of a turtle can alter the form of its movement (Valk-Fai and Crowe, 1979; Stein and Grossman, 1980). Proprioceptive information signalling the position of the scratching leg can therefore regulate activity of the central pattern generator that drives scratching in both the cat and turtle.

Intact frogs can use a hindleg to scratch the other hindleg or

*e-mail: tm114@hermes.cam.ac.uk.

the ipsilateral foreleg, regardless of the position of the target leg (within a range of possible positions defined by mechanical constraints), indicating that proprioceptive sensory information from the target leg is also able to influence the motor output that underlies targeting of the scratching leg (Fukson *et al.* 1980; Giszter *et al.* 1989). Intact frogs have a preferred leg posture for hindleg-hindleg scratching, but can nevertheless target locations throughout the range of possible positions (Giszter *et al.* 1989). Spinalised frogs produce more stereotyped movements in which both the target and scratching legs are positioned at particular initial locations relative to the body and moved through accurate and repeatable postures at critical points of the response (Giszter *et al.* 1989). If the target leg is restrained near to the preferred position, frogs scratch successfully, but as the leg is restrained progressively further away, the movements become erratic or stop, indicating that spinal frogs cannot adapt the trajectory of the scratching leg to account for imposed changes in target position (Giszter *et al.* 1989). The question posed in the present paper is whether an arthropod, the locust *Schistocerca gregaria*, can adjust its leg targeting during scratching to account for alterations in stimulus position when a target wing is moved from its resting posture to an outstretched posture similar to that used during flight.

Arthropods make a variety of coordinated movements of the legs and body segments to clean the surface of the body (cricket, Honegger *et al.* 1979; Hensler and Honegger, 1985; cockroach, Eaton and Farley, 1969; locust, Rowell, 1961; O'Shea, 1970), including scratching movements of the hindlegs (locust, Meyer, 1993) or middle legs (locust, Berkowitz and Laurent, 1995). Intact locusts respond to tactile stimulation of their folded wings with scratching movements of their hindlegs that are directed towards the site of stimulation, so that different sites of stimulation along the wing elicit different patterns of leg movements (Meyer, 1993). Other patterns of muscle activity drive the hindleg to scratch the ear or the posterior end of the abdomen (Berkowitz and Laurent, 1995).

Motor neurones that control movements of the hindlegs of a locust are located in the metathoracic ganglion (e.g. Wilson, 1979), which also receives sensory inputs from tactile receptors on the hind wing. Sensory neurones from the forewing enter the mesothoracic ganglion (e.g. Elliot, 1983) and the information that they carry is passed posteriorly to the metathoracic ganglion *via* the intersegmental connectives. Locusts whose meso- and metathoracic ganglia are isolated from more anterior ganglia by section of the connectives anterior to the mesothoracic ganglion still produce correctly targeted scratching (Berkowitz and Laurent, 1995), indicating that the head ganglia are not required for this behaviour.

The present work demonstrates that although intact locusts direct a hindleg to scratch the appropriate stimulus sites along the length of the ipsilateral wings, they fail to alter this targeting when the wings are held outstretched orthogonal to the body axis, and thus scratch at empty points in space. This inappropriate scratching in response to tactile stimulation of an outstretched wing also occurs when the metathoracic ganglion, which controls the hindleg, is isolated from the remainder of the CNS.

Materials and methods

Locusts (*Schistocerca gregaria* Forskål) from our crowded colony were tethered above a light foam ball (diameter 8 cm) so that they could stand or walk in any direction while being videotaped using a Sony CCD TR2000E Hi-8 video camera. They were tethered either by a solid yoke waxed to the dorsal pronotum or by a flexible wire loop passed around the neck anterior to the mesothoracic legs. Both methods allowed the animals unhindered movements of their legs and wings. The eyes were covered with typists' white correction fluid to prevent any possible influence of visual input on leg targeting and to reduce struggling. Covering the eyes in this way did not alter leg targeting during scratching.

Movements of locusts were videotaped from a lateral view, and from a dorsal view using a mirror mounted at 45° above the walking ball. Hi-8 videotapes were copied to VHS format and played back for frame-by-frame analysis on a Panasonic AG-6200 recorder and WV-5410 monitor. The following results are based on videotaped observations of 454 scratches in 20 locusts. Each scratch was scored according to whether the tarsus of the hindleg ipsilateral to the stimulus passed across the stimulus site. For 11 scratches, the positions of the base of the tarsus of the ipsilateral hindleg were plotted for each frame (25 frames s^{-1}), and the stimulus site was recorded. The apparent direction of walking could be determined by observing movements of the ball. In the Figures, the mirror image recorded has been re-inverted for clarity.

Scratching was elicited by gently touching a wing with a fine paintbrush. The stimulus site was, at most, 10 mm in diameter. Such stimuli will activate many sensory receptors, including trichoid sensilla, the mechanoreceptive neurones of basiconic sensilla, campaniform sensilla and perhaps proprioceptors such as the chordotonal organ and stretch receptor at the base of the wing. When the wings are folded, each forewing completely covers the ipsilateral hindwing, so touching the lateral (upper) surface of a forewing is likely to stimulate tactile receptors of both ipsilateral wings: those of the hindwing indirectly through movements of the forewing. Similarly, movements of a wing caused by the stimulus could be transmitted to mechanoreceptors on the abdomen, so in some experiments these abdominal sensory pathways were ablated by sectioning the connectives that link the abdominal ganglia with the metathoracic ganglion, and the abdominal nerves entering the metathoracic ganglion (which contains the fused metathoracic and first three abdominal neuromeres). The metathoracic ganglion was further isolated by also cutting the connectives that link it with the mesothoracic ganglion. To perform these ablations, locusts were first restrained ventral-surface uppermost and a flap was cut in the thoracic cuticle overlying the metathoracic ganglion. The appropriate nerves and connectives were cut, the thorax was resealed by waxing the

flap of cuticle back into position, and the locusts were tethered above the walking ball.

The forewings of intact locusts were touched at different sites to confirm that scratching movements are targeted at points along the length of the wing, as reported by Meyer (1993). A forewing was then held outstretched with its distal tip elevated and lateral to the point of attachment to the thorax, stimulated at the same points as before and the scratching movements were recorded. In other experiments, a forewing was held outstretched immediately after tethering an animal so that scratching was first elicited with the wing in this position. The order of stimulation had no effect on the movements described below. In some experiments, a hindwing was held outstretched along with the ipsilateral forewing and could be touched to elicit scratching, or all the wings except one forewing were removed by cutting through them near their bases. When a hindwing was held outstretched, its trailing edge was trimmed so that the ipsilateral hindleg did not touch it.

In experiments using animals with an isolated metathoracic ganglion, tactile stimulation was restricted to a hindwing because sensory pathways from the forewings to the metathoracic ganglion (*via* the mesothoracic ganglion) were removed by the ablations.

Results

Intact locusts tethered above the walking ball assumed a characteristic posture with the wings folded along the abdomen and the legs arrayed laterally (Fig. 1).

Holding a wing or both ipsilateral wings outstretched caused the animals to struggle for a short period (usually no longer than 1 min), but they then remained quiet, groomed their mouthparts or walked.

Scratching elicited with wings folded

Touching the wings of locusts could elicit a range of movements of the wings, body or legs, but only those movements defined here as hindleg scratching are the subject of this study. This scratching behaviour consisted of rapid directed movements of the ipsilateral hindleg generated by coordinated extension and flexion movements of three joints: the thoraco-coxal, femoro-tibial and tibio-tarsal (see Meyer, 1993; Berkowitz and Laurent, 1995). The number of cycles per scratch ranged from 1–11 (*N*=454 scratches in 20 animals) and the approximate duration of a single cycle was 550±36 ms (mean ± S.E.M., from a representative sample of four scratches in four animals).

During scratching behaviour, the tarsus of the scratching leg was passed across the stimulus site on the wing (Fig. 1). The behaviour differed from kicking, which is characterised by a period of complete tibial flexion followed by a single rapid tibial extension (Heitler and Burrows, 1977); and from pushing and struggling movements, which consisted of larger amplitude and more variable extensions and flexions of a
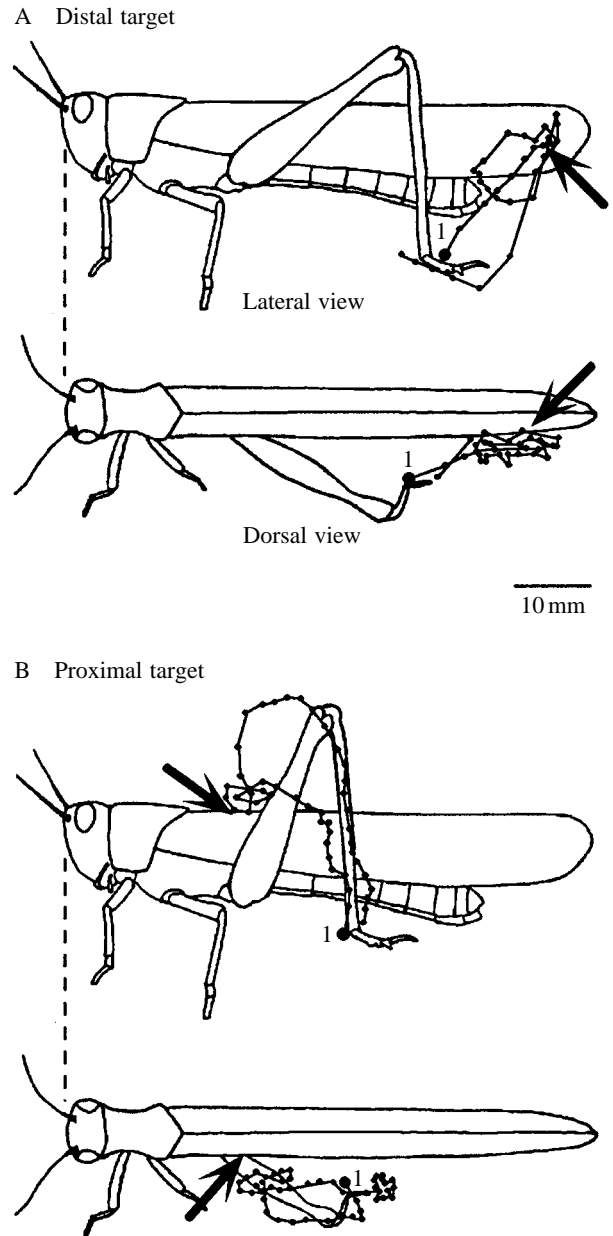

Fig. 1. (A) Lateral (upper) and dorsal (lower) views of an intact locust scratching with a left hindleg in response to tactile stimulation of the distal end of the left forewing (arrow). Sequential positions of the tarsus were plotted at 40 ms intervals, beginning at the point labelled 1. (B) Corresponding views of a locust scratching in response to stimulation near the base of the forewing.

hindleg accompanied by movements of other legs, the wings and/or the abdomen.

Touching different stimulus sites along a forewing elicited different patterns of scratching, so that the ipsilateral hindleg tarsus moved towards the appropriate stimulus position. Touching the distal tip of a forewing elicited a movement in which the tarsus was lifted from the ground, primarily by femoral levation, then moved posteriorly and medially, primarily by tibial extension and coxal rotation, directly across the stimulus site (Fig. 1A). The tarsus then followed a looping

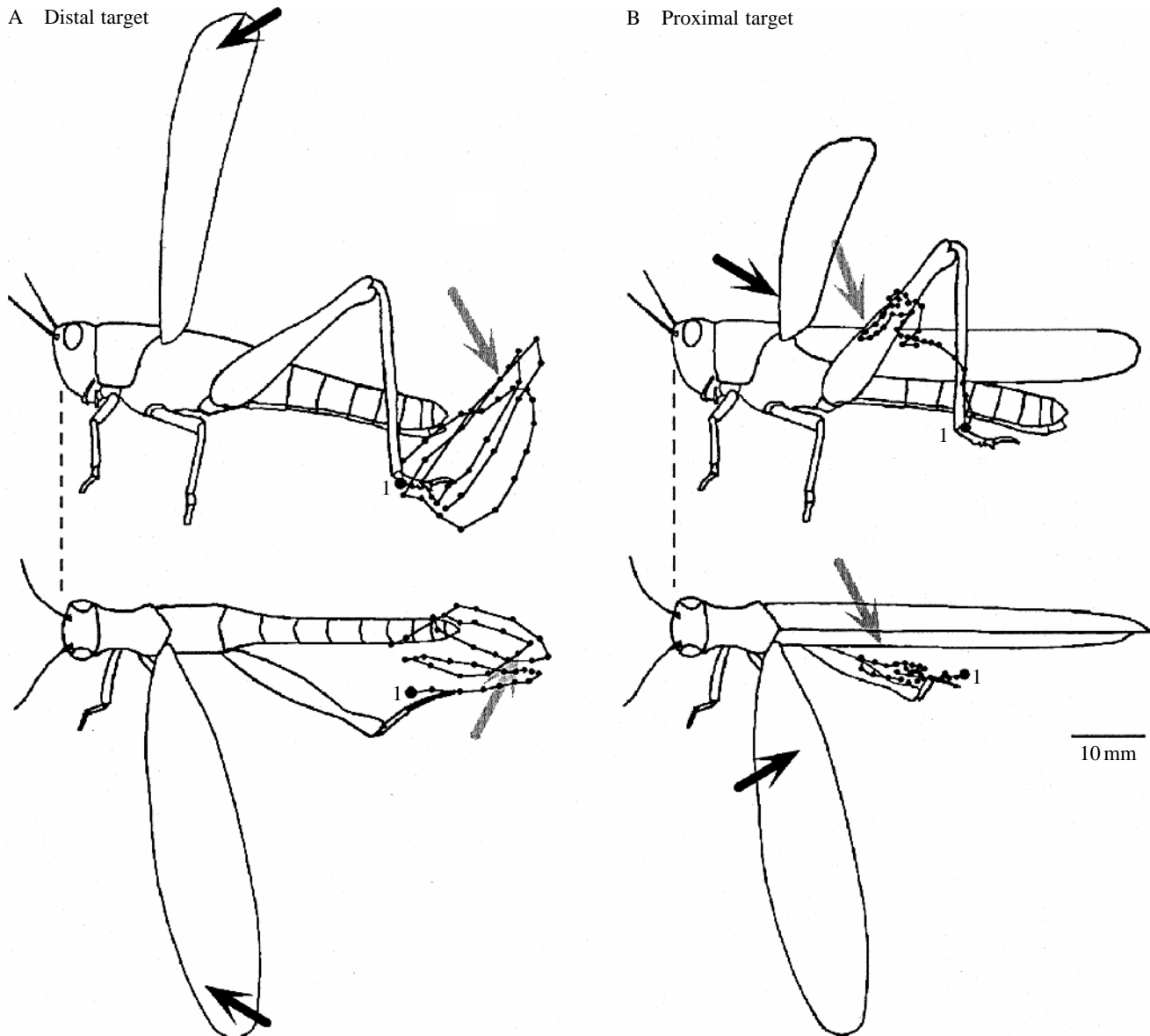A   Distal target

B   Proximal target

Fig. 2. (A) Lateral (upper) and dorsal (lower) views of a locust scratching with a left hindleg in response to tactile stimulation of the distal end of the left forewing (solid arrow), which was held outstretched. The ipsilateral hindwing and both contralateral wings were removed. Stippled arrows indicate where the stimulus site would have been if the wing was folded in the normal rest posture. (B) Corresponding views of a locust scratching in response to stimulation near the base of a forewing. The wing is slightly less elevated in B than in A.

path ventrally and anteriorly as the tibia was flexed, before again passing across the stimulus site during tibial extension. In contrast, touching a forewing near to its base elicited a movement in which the tarsus was moved further anterior by a rotation of the coxa while the tibia was held flexed, before passing across the stimulus site during tibial extension and returning to the rest position (Fig. 1B).

Intact locusts hit the target site in 93 % of scratches (*N*=131 scratches in 15 animals).

Scratching elicited with wings outstretched

Touching a forewing that was held outstretched, with the other wings intact or removed, also led to scratching movements with a similar form, but these were never directed at the stimulus site on the outstretched wing (*N*=323 scratches in 11 animals). Instead, they were directed towards where the stimulus site would have been were the wing to have remained folded in its resting posture (Fig. 2A,B), so that the locust scratched at an empty point in space near the abdomen. Touching different sites on the outstretched wing continued to elicit site-specific patterns of scratching, however: stimulus sites at the distal end of the wing produced scratching movements distal to the posterior end of the abdomen in 97 % of trials (Fig. 2A), and stimulus sites within 20 mm of the base of the wing produced scratching at more anterior positions (within 10 mm of the thorax) in 39 % of trials (*N*=11 animals) (Fig. 2B). In the example shown in Fig. 2A, the ipsilateral hindwing and both contralateral wings

A   CNS intact

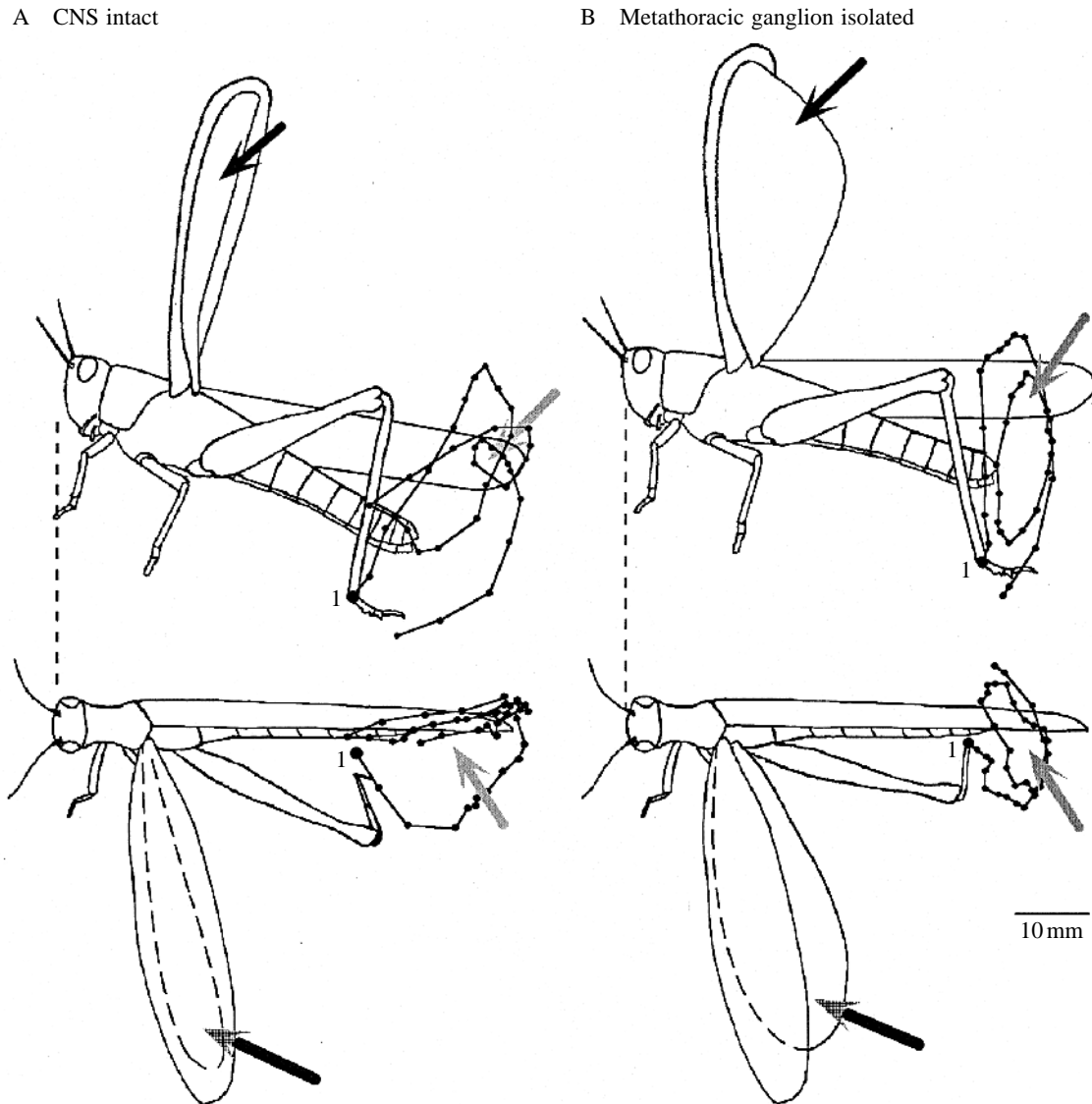B   Metathoracic ganglion isolated

10 mm

Fig. 3. (A) Lateral (upper) and dorsal (lower) views of an intact locust scratching with a left hindleg in response to tactile stimulation (solid arrow) of the undersurface of the distal end of the left hindwing, which was held outstretched along with the overlying forewing. (B) Corresponding views of a locust whose metathoracic ganglion was first isolated from the rest of the CNS by ablation of the anterior and posterior connectives and abdominal nerves. Stippled arrows indicate where the stimulus site would have been if the wings were folded in the normal rest posture.

were removed to preclude the possibility that the animal was responding to mechanical stimuli transmitted to their tactile receptors.

Tactile stimulation of the distal end of a hindwing that was held outstretched along with the ipsilateral forewing also elicited scratching near the distal end of the abdomen (Fig. 3A).

Although holding a wing outstretched had no effect on the targeting of scratching movements, it did affect walking behaviour: six out of seven locusts with outstretched wings consistently turned away from the side that had been manipulated, whereas only one of these animals consistently turned away from the stimulated side when the wings were folded in the rest position. Turning occurred between scratches

throughout the test period, indicating that at least some wing sensory systems did not adapt to the outstretched position.

Animals that were aroused by prolonged tactile stimulation of the body, legs and wings made a wide variety of struggling, pushing and kicking movements with their hindlegs, during some of which the tarsus reached an outstretched wing (results not shown). The failure to reach an outstretched wing during scratching cannot therefore be due to mechanical constraints on movements of the hindlegs.

Scratching elicited in animals with an isolated metathoracic ganglion

In five animals, the abdominal connectives and nerves were cut to remove sensory input from abdominal sensory receptors;

the connectives anterior to the metathoracic ganglion were cut to rule out both descending inputs from anterior ganglia including the brain and sensory inputs from the forewing. In all five animals, tactile stimulation of the distal end of a hindwing still elicited scratching near the posterior end of the abdomen, regardless of whether the wing was folded at rest or held outstretched (Fig. 3B).

Discussion

Locusts target their scratches at sites of tactile stimulation on a wing in such a way that the tarsus crosses the point of stimulation, and different sites of stimulation elicit different patterns of leg movement (Meyer, 1993). The interpretation is that sensory information from arrays of mechanoreceptors on the surface of the wing encodes the stimulus position, and this representation is used by the CNS to generate these accurately targeted leg movements.

The present study shows that locusts use positional information from an array of receptors on one appendage (a forewing or a hindwing) to guide scratching movements made by another (the ipsilateral hindleg). More important is the demonstration that a locust is unable to alter its scratching behaviour to compensate for imposed movements of the target wing, and therefore exhibits an inappropriate response.

When a wing of a locust was held away from its normal resting posture while it was touched with a paintbrush, the locust scratched at a point in space that was near to where the stimulus site would have been if the wing was folded in its resting posture. If the stimulus site was moved along the length of the outstretched wing then the scratching movements changed in a corresponding way so that sites near the distal end of the outstretched wing elicited scratches near the posterior end of the abdomen whereas stimulus sites near the base of the wing elicited scratches near the thorax. The leg targeting mechanism, although functioning, did not take into account the altered orientation of the wing. The failure to scratch laterally is not a result of mechanical constraints on the movement, as indicated by the observation that locusts aroused by prolonged tactile stimulation could make wide dorsal and lateral sweeping movements with their hindlegs that reached an outstretched wing.

The use of positional information to target insect leg movements has previously been documented in studies of other grooming behaviours. For example, cleaning movements of the forelegs are elicited by stimulating sensory receptors on the prothoracic spine or antennae of a locust (Rowell, 1961; O'Shea, 1970), or eyes of a cricket (Honegger et al. 1979). Stimulating mechanosensitive bristles on the notum or tegula of Drosophila elicits different patterns of leg movement depending on the position of the receptor (Vandervorst and Ghysen, 1980): stimulation of anterior receptors evokes cleaning movements of a foreleg, whereas posterior receptors evoke cleaning movements of a hindleg. Stimulation of ectopic bristles in mutant Drosophila (*wingless* or *bithorax postbithorax* mutations) elicits leg movements that are identical to those elicited by stimulation of the homologous but normally located bristles.

Eye grooming in crickets and antennal grooming in locusts are achieved by coordinated movements of the forelegs and head, which rolls towards the side being groomed (Honegger et al. 1979; O'Shea, 1970). If the head of a locust is prevented from moving by being waxed to the thorax then the animal can adjust the grooming movements of its foreleg to reach the antenna (O'Shea, 1970). In the cricket, however, waxing the head in a similar way usually prevents an animal from reaching its eye with its foreleg (Honegger et al. 1979). In these studies it is not clear to what extent mechanical rather than neural considerations produced the observed outcomes.

Although the sensory receptors responsible for eliciting some forms of grooming have been identified (e.g. Honegger et al. 1979), it is not known which central neurones receive and process this information. The sensory basis for different site-specific leg avoidance reflexes of a locust, however, can be explained by the tactile receptive fields of its leg motor neurones (Burrows and Siegler, 1985; Siegler and Burrows, 1986). Touching tactile hairs on the ventral surface of a hindleg tibia causes a reflex elevation of the femur, extension of the tibia and depression of the tarsus; whereas stimulation of hairs on the dorsal surface of the tibia results in femoral levation but tibial flexion. These different movements involving muscles of at least three joints of the leg serve to move it away from the point of stimulation. Motor neurones that innervate these muscles have receptive fields consisting of arrays of receptors on the leg, and the particular array of receptors defines how the motor neurone responds to a touch on different surfaces of the leg. For example, the slow extensor tibiae motor neurone, which contributes to tibial extension, is excited by tactile hairs on the ventral distal femur and ventral tibia, and inhibited by hairs on the corresponding dorsal surfaces (Siegler and Burrows, 1986).

It is most likely that the scratching described in the present study is evoked by stimulation of the many tactile hairs scattered across both surfaces of the wings. Hairs on the forewing project to the mesothoracic ganglion whereas those on the hindwing project to the metathoracic ganglion that contains motor neurones responsible for generating movements of the hindleg. Results from the present study show that a locust with an isolated metathoracic ganglion can generate a targeted scratch, and that an intact locust can use sensory information entering the CNS in different body segments to generate hindleg movements targeted at a single point in space, i.e. near the distal end of the abdomen (compare Fig. 2A with Fig. 3A). Our detailed understanding of the sensory and motor networks underlying locust leg movements (reviewed by Burrows, 1992, 1994) means that we are now in a good position to investigate how this parallel inflow of sensory information is processed in two ganglia to produce targeted movements generated within a single ganglion.

Many types of sensory structures monitor the position and movements of a locust wing, and could thus signal its outstretched position. These include a multiterminal stretch receptor, a chordotonal organ, groups of campaniform sensilla

(reviewed by Wright, 1976), and the tegula, which is a sensory structure consisting of another chordotonal organ and arrays of tactile hairs (Kutsch *et al.* 1980). The stretch receptor provides information concerning wing elevation (Gettrup, 1962), the wing chordotonal organ may signal wing depression (Gettrup, 1962; *cf.* Pearson *et al.* 1989), while the campaniform sensilla provide information that gives the animal fine control over the amount of wing twisting (Gettrup and Wilson, 1964; Gettrup, 1966). Tegula afferents signal wing downstroke (Neumann, 1985). Tactile hairs on the lower surface of the forewing or upper surface of the hindwing could signal whether the wings are folded into their resting posture by detecting mutual contact of the wings. The observation that locusts turned away from the side being manipulated indicates that at least some of these sensory receptors signal the outstretched position of a wing throughout the period of testing. It seems unlikely that this turning is simply a mechanical effect, because to turn away from the manipulated wing requires that the legs on that side make larger and more powerful steps than those on the contralateral side. A more likely interpretation is that sensory information from wing or thoracic receptors signals the disturbance of the wing and influences the stepping motor pattern.

In a flying locust, wing proprioceptive information permits fine control of wingbeat timing, steering and lift, yet a scratching locust appears not to use such information to either alter leg targeting or to inhibit inappropriate behaviour. In a decerebrate cat, fictive scratching can only be elicited if the 'scratching' leg is held near to its normal scratching posture. If the leg is held in an unusual posture, the scratching motor activity stops (Berkinblit *et al.* 1978), indicating that proprioceptive information from the scratching leg can act as a gate for this behaviour. Intact frogs can accurately scratch one hindleg with the other, even when the target leg is held in an unusual position (Fukson *et al.* 1980; Giszter *et al.* 1989), so proprioceptive information from the target leg must be used to compute the altered target position. A spinal frog, however, cannot compensate for such alterations in target leg topography (Giszter *et al.* 1989). These observations suggest that the ability to take alterations of target limb position fully into account when computing a movement strategy requires supraspinal centres in vertebrates, and is absent in a locust.

Resting locusts rarely, if ever, hold their wings in an outstretched flight posture, so they should have no need to scratch at these spatial locations. Flying locusts, on the other hand, should not scratch at all as this would conflict with aerodynamic requirements and may lead to damage of the fragile hindwings. It is surprising, therefore, that resting locusts whose wings are held outstretched continue to scratch at an inappropriate target site, rather than refraining from scratching or switching to other behaviours such as kicking or struggling.

References

BERKINBLIT, M. B., DELIAGINA, T. G., FELDMAN, A. G., GELFAND, I. M. AND ORLOVSKY, G. N. (1978). Generation of scratching. II. Nonregular regimes of generation. *J. Neurophysiol.* **41**, 1058–1069.

BERKOWITZ, A. AND LAURENT, G. J. (1995). Central generation of directed limb movements in locusts. *Soc. Neurosci. Abs.* **21**, 696.1.

BURROWS, M. (1992). Local circuits for the control of leg movements in an insect. *Trends Neurosci.* **15**, 226–232.

BURROWS, M. (1994). The influence of mechanosensory signals on the control of leg movements in an insect. In *Neural Basis of Behavioural Adaptations* (ed. K. Schildberger and N. Elsner), pp. 145–165. Stuttgart, Jena, New York: Gustav Fischer Verlag.

BURROWS, M. AND SIEGLER, M. V. S. (1985). The organization of receptive fields of spiking local interneurones in the locust with inputs from hair afferents. *J. Neurophysiol.* **53**, 1147–1157.

DELIAGINA, T. G., FELDMAN, A. G., GELFAND, I. M. AND ORLOVSKY, G. N. (1975). On the role of central program and afferent inflow in the control of scratching movements in the cat. *Brain Res.* **100**, 297–313.

EATON, R. C. AND FARLEY, R. D. (1969). The neural control of the cercal grooming behaviour in the cockroach, *Periplaneta americana. J. Insect Physiol.* **15**, 1047–1065.

ELLIOT, C. J. H. (1983). Wing hair plates in crickets: physiological characteristics and connections with stridulatory motor neurones. *J. exp. Biol.* **107**, 21–47.

FUKSON, O. I., BERKINBLIT, M. B. AND FELDMAN, A. G. (1980). The spinal frog takes into account the scheme of its body during the wiping reflex. *Science* **209**, 1261–1263.

GETTRUP, E. (1962). Thoracic proprioceptors in the flight system of locusts. *Nature* **193**, 498–499.

GETTRUP, E. (1966). Sensory regulation of wing twisting in locusts. *J. exp. Biol.* **44**, 1–16.

GETTRUP, E. AND WILSON, D. M. (1964). The lift-control reaction of flying locusts. *J. exp. Biol.* **41**, 183–190.

GISZTER, S. F., MCINTYRE, J. AND BIZZI, E. (1989). Kinematic strategies and sensorimotor transformations in the wiping movements of frogs. *J. Neurophysiol.* **62**, 750–767.

HEITLER, W. J. AND BURROWS, M. (1977). The locust jump: I. the motor programme. *J. exp. Biol.* **66**, 203–219.

HENSLER, K. AND HONEGGER, H.-W. (1985). Activity of neck-muscle motoneurones during eye cleaning behaviour in the cricket *Gryllus campestris. J. Insect Physiol.* **31**, 425–433.

HONEGGER, H.-W., REIF, H. AND MÜLLER, W. (1979). Sensory mechanisms of eye cleaning behavior in the cricket *Gryllus campestris. J. comp. Physiol.* A **129**, 247–256.

KUTSCH, W., HANLOSER, H. AND REINECKE, M. (1980). Light- and electron-microscopic analysis of a complex sensory organ: the tegula of *Locusta migratoria. Cell Tissue Res.* **210**, 461–478.

MEYER, T. S. (1993). Patterns of activity in metathoracic leg muscles during rhythmic scratching behaviour in the locust. *XXXII IUPS*, 280.10/P.

MORTIN, L. I., KEIFER, J. AND STEIN, P. S. G. (1985). Three forms of scratch reflex in the spinal turtle: movement analyses. *J. Neurophysiol.* **53**, 1501–1516.

NEUMANN, L. (1985). Experiments on tegula function for flight coordination in the locust. In *Insect Locomotion* (ed. M. Gewecke and G. Wendler), pp. 149–156. Berlin, Hamburg: Paul Parey.

O'SHEA, M. (1970). The antennal cleaning reflex in the desert locust, *Schistocerca gregaria* (Forsk.). *Proc. Int. Study Conf. Current and Future Problems of Acridology, London*, pp. 55–59.

PEARSON, K. G., HEDWIG, B. AND WOLF, H. (1989). Are the hindwing

chordotonal organs elements of the locust flight pattern generator? *J. exp. Biol.* **144**, 235–255.

ROBERTSON, G. A., MORTIN, L. I., KEIFER, J. AND STEIN, P. S. G. (1985). Three forms of scratch reflex in the spinal turtle: central generation of motor patterns. *J. Neurophysiol.* **53**, 1517–1534.

ROWELL, C. H. F. (1961). The structure and function of the prothoracic spine of the desert locust, *Schistocerca gregaria. J. exp. Biol.* **38**, 457–469.

SHERRINGTON, C. S. (1906). Observations on the scratch-reflex in the spinal dog. *J. Physiol., Lond.* **34**, 1–50.

SHERRINGTON, C. S. (1910). Notes on the scratch-reflex of the cat. *Q. J. exp. Physiol.* **3**, 213–220.

SIEGLER, M. V. S. AND BURROWS, M. (1986). Receptive fields of motor neurons underlying local tactile reflexes in the locust. *J. Neurosci.* **6**, 507–513.

STEIN, P. S. G. (1983). The vertebrate scratch reflex. In *Neural Origin of Rhythmic Movements*, vol. 37 (ed. A. Roberts and B. Roberts), pp. 383–403. Cambridge: Cambridge University Press.

STEIN, P. S. G. AND GROSSMAN, M. L. (1980). Central program for scratch reflex in turtle. *J. comp. Physiol.* A **140**, 287–294.

VALK-FAI, T. AND CROWE, A. (1979). Further analyses of reflex movements in the hind limb of the terrapin *Pseudemys scripta elegans. J. comp. Physiol.* A **130**, 241–249.

VANDERVORST, P. AND GHYSEN, A. (1980). Genetic control of sensory connections in *Drosophila. Nature* **286**, 65–67.

WILSON, J. A. (1979). The structure and function of serially homologous leg motor neurons in the locust. I. Anatomy. *J. Neurobiol.* **10**, 41–65.

WRIGHT, B. R. (1976). Limb and wing receptors in insects, chelicerates and myriapods. In *Structure and Function of Proprioceptors in the Invertebrates* (ed. P. J. Mill), pp. 323–386. London: Chapman and Hall.