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Wing hair sensilla underlying aimed hindleg scratching of the locust

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Summary

The anatomy and physiology of exteroceptors on the surfaces of the wings have been described in many insects, but their roles in behaviour have been less well studied. They have often been assumed to have a role primarily in flight. We show that the wings of the locust *Schistocerca gregaria* possess at least three different hair types with characteristic patterns of distribution that determine the probability of eliciting targeted hindleg scratching behaviour.

The different hair types are defined by their morphology and innervation. The shortest hairs (14–46 μm) are basiconic receptors containing both chemosensory and mechanosensory afferents. They are distributed widely across the dorsal surfaces of the forewings; some are located on the ventral surfaces of the hindwings, but none are found on the ventral surfaces of the forewings or the dorsal surfaces of the hindwings. Medium length hairs (73–159 μm) are found on all wing surfaces, but are restricted to the veins, principally the subcosta on the dorsal surface of the forewings. The longest hairs (316–511 μm) are found only on the postcubitus vein on the dorsal surfaces of the forewings, so that they form a pair of dorsal rows when the wings are folded at rest.

Touching the dorsal surface of a forewing can elicit aimed scratching movements of a hindleg, and we show that the probability of eliciting a scratch differs for different stimulus sites and for different start positions of the hind leg. The effectiveness of different stimulus sites can be correlated with the distribution of tactile hairs on the dorsal forewing surface. Touching the long hairs provides the strongest drive to elicit a scratch, and ablating them reduces the probability to almost zero. We conclude that input from forewing tactile hairs plays an important role in eliciting hindleg scratching and encodes the spatial location required for targeting.

Key words: *Schistocerca gregaria*, wing, tactile hair, basiconic sensillum, scratching.

Introduction

The body surfaces of insects are richly endowed with trichoid exteroceptors of many types (McIver, 1975). These include mechanosensory hairs of different lengths, which respond to touch or to air movements (Newland, 1991); chemosensory hairs with pores in their tips (basiconic sensilla) that respond to contact with chemicals (Maes and Hams, 1986: White et al., 1990); and olfactory hairs that respond to airborne volatiles (Slifer, 1954; Slifer and Finlayson, 1956). The latter are primarily restricted to the antennae, but the former two types occur widely across the body surface. Stimulation of mechanosensory or chemosensory hairs on different regions of the body elicits behaviourally relevant responses so that, for example, touching the hairs on a locust leg can elicit a leg withdrawal movement, but touching hairs on the cockroach cercus can elicit an escape run (Camhi and Tom, 1978). Stimulation of tactile hairs on the legs, eyes and antennae of insects can cause a variety of local or intersegmental reflexes (Rowell, 1969; O'Shea, 1970; Honegger, 1979; Pflüger, 1980; Siegler and Burrows, 1986; Burrows, 1989; Newland, 1998).

In contrast to our detailed knowledge about the anatomy, physiology and behavioural roles of trichoid hairs on the body and legs (e.g. Burrows, 1996), surprisingly little is known about the hairs on the wings. Each locust hindwing possesses 12 400 hairs and bristles scattered across its veins and membrane (Altman et al., 1978). Only some 800 of these are innervated, and their sensory neurones project as small diameter axons in nerve 1A into the metathoracic ganglion (Altman et al., 1978). The forewings are smaller than the hindwings and have a thickened cuticle. At rest they protect the delicate hindwings that lie folded beneath them (Wootton et al., 2000). The distribution and innervation of trichoid hairs on the forewings of locusts has not been described satisfactorily.

The single study of the forewing hairs of a locust (*Locusta migratoria*), described only one type of small trichoid hair, up to 40 μm long, which were restricted to the principal veins (Knyazeva, 1970). Hairs of over 100 μm length were recorded on the tegulae and articular sclerites, whereas hairs of over 300 μm were only present on the cuticle of the pterothorax

(Knyazeva, 1970). In contrast, our observations of ten specimens of *Locusta migratoria* provided by a commercial supplier (Blades Biological, Edenbridge, UK) revealed hairs of up to 215±37.6 μm on veins near the leading edge of the forewing (K.P., personal observations). The trichoid hairs on the forewing surface were assumed by Knyazeva (1970) to "*have some significant role for flight and [to] perceive the pressure of the air stream on the moving wing*", although this was not tested. Since the numbers of strain-sensitive campaniform sensilla on the wings and tegula, and tegula hairs, are generally higher in good fliers than in species with poor flying ability, the presence of these wing receptors has been linked to the control of flight behaviour (Knyazeva, 1986a,b). This assumed role in flight is repeated in studies of the wing hairs of the cricket *Gryllus domesticus* (Fudalewicz-Niemczyk and Rosciszewska, 1972), the grasshopper *Melanoplus sanguinipes* (Albert, 1976), and in a series of studies by Knyazeva on grasshopper *Stauoderus biguttulus* (Zaćwilichowski, 1934b); stonefly *Isopteryx tripunctata* (Zaćwilichowski, 1936), and cockroaches *Phyllodromia germanica* (Zaćwilichowski, 1934a) and *Periplaneta americana* (Knyazeva, 1976a). In the nocturnal cockroach *Phyllodromia germanica* the many wing hairs were suggested to have chemosensory and mechanosensory roles (Knyazeva, 1934), but in *Periplaneta americana*, since both the hairs and the campaniform sensilla are restricted to the wing veins, which are axes of mechanical strength, Knyazeva (1976a,b) speculated that these wing hairs might have a role in flight.

The small axon diameters and low conduction velocities of the sensory neurones that innervate hairs on the hindwing, and presumably also those on the forewing, make it unlikely that these receptors are involved in rapid reflex control or tuning the flight motor pattern on a single wing-beat time scale (Gettrup, 1965; Burrows, 1996). Little is known of the activity of forewing hair afferents during flight (Wilson, 1961; Gettrup, 1965). The synaptic connections made by trichoid hair afferents from the locust forewing have not been described, so it is unclear whether their signals are primarily used by leg motor networks, flight control networks or both. Some exteroceptive sensory inputs from the forewings, however, have been shown to converge along with proprioceptive inputs from the ipsilateral hindleg onto spiking local interneurones from a population that is involved in generating leg reflexes (Matheson, 2002).

Touching a forewing or a hindwing of a locust can elicit an aimed grooming behaviour in which one or both hindlegs move towards the point of stimulation, often in a cyclical trajectory (Meyer, 1993; Berkowitz and Laurent, 1996a; Matheson, 1997, 1998, 2003). This scratching behaviour might help to keep the wing surface clean or it might enable a locust to fend off a predator or conspecific. The wing receptors underlying aimed scratching have not been demonstrated, but the most likely candidates are the trichoid hairs, since no other receptors are distributed across the surface in a way that could easily signal the location of a touch. In crickets, touching the surface of a hindwing can elicit an escape response, which is mediated by one class of twisted trichoid hairs (Hiraguchi and Yamaguchi, 2003).

In this paper we describe the distribution of three classes of trichoid hairs on the wings of the locust *Schistocerca gregaria*. We show that, of these, a row of the longest tactile hairs on the forewings was particularly effective in eliciting hindleg scratching. Stimulation of the other tactile hairs can also elicit scratching, but stimulation of the chemoreceptive afferents in basiconic receptors was relatively ineffective.

Materials and methods

Distribution of exteroceptors on the forewings

Adult male and female desert locusts *Schistocerca gregaria* Forskål were taken from the crowded colony maintained at the Department of Zoology, University of Cambridge. Forewings from five males and five females were removed and the dorsal surface coated in clear nail polish. The dry coating was then peeled off to give a transparent cast of the dorsal surface, with a clear impression of the cuticle and sensilla (Rogers et al., 2003). The casts were drawn at 62× magnification using a camera lucida attached to a dissection microscope and the hairs were marked and counted. Parametric statistical tests (multivariate analysis of variance MANOVA and analysis of variance ANOVA) were carried out on hair numbers using SPSS version 10 for Windows (SPSS Inc.). Terminology for wing veins is from Albrecht (1953). We refer to the wing long axis as proximal–distal and the orthogonal axis as leading–trailing. The wing surfaces are referred to as dorsal and ventral to reflect their orientation in flight.

The forewings of females are longer than those of males, so hair counts were expressed as hairs per cm. Basiconic sensilla are not restricted to longitudinal veins, so their counts were expressed as hairs per cm^2. Photographs were taken using a Nikon E995 (Kingston, UK) Coolpix digital camera attached to a dissection microscope.

Structure of exteroceptors

Individual forewings were removed from another five female locusts, rinsed in distilled water in a sonicator to remove dust and debris, and then dried at room temperature. Small (5 mm square) portions were then dry-mounted on aluminium stubs, sputter-coated with gold, and examined using a Philips (Croydon, UK) scanning electron microscope (SEM). Forty-six hairs on the dorsal surface were photographed and their lengths measured. Care was taken to adjust the angle of view so that it was orthogonal to the axis of each hair measured. The distribution of hair lengths formed the basis for the three length categories used in this paper.

Physiological recordings

Isolated fore- and hindwings were secured in modelling clay. Hair afferents were stimulated and recorded using a modification of the 'tip recording' technique (Hodgson, 1955). A reference electrode was placed into the main wing vein at the cut base of the wing, and a broken glass microelectrode,

filled with locust saline (or saline with additional sodium chloride to 100 mmol l^{-1}, and sucrose to 250 mmol l^{-1}) was placed over the intact hair tip. Signals were recorded using standard amplifiers and captured to computer using a CED1401 interface and Spike2 software (Cambridge Electronic Design, Cambridge, UK). Basiconic receptors were easily identified by their multiple innervation, reflected in multiple spike amplitudes in recordings from intact receptors. If no response was detected from an intact hair, then it was classed as being not basiconic and its tip was cut off before another recording was attempted. Mechanosensory hairs were recognised by spikes of a single amplitude in response to movements of the recording electrode. If cutting the hair shaft failed to reveal spiking activity then the hair was cut closer to the cuticle and recording attempted again. In the absence of activity the hair was classed as non-innervated. Over 50 recordings were made from short hairs, severed medium length hairs, severed long hairs and non-innervated hairs across both surfaces of fore- and hindwings of 8 animals.

Probability of eliciting a scratch

Five male and five female locusts were tethered using a wire noose around the pronotum, and each given a polystyrene ball of 5 cm diameter, on which they could walk freely (Matheson, 1997). The eyes and ocelli were blacked out using water-based black acrylic paint (Daler-Rowney, Acryla; Bracknell, UK). The ten animals were set up together and allowed to rest for 30 min before the experiment began. A 3 mm diameter start pole provided a footrest on which the right-hand hindleg tarsus stood at the beginning of each stimulus. This start pole was positioned at 2/5 (anterior position) or 4/5 (posterior position) of the distance between the metathoracic coxal joint and the distal tip of the wing, ventral to the abdomen (Dürr and Matheson, 2003). The wing area was subdivided notionally along the proximal–distal axis (which lies anterior–posteriorly when the wings are folded at rest) into five bins of equal length, the four most proximal of which were then subdivided into leading and trailing edge regions (which lie dorso–ventrally when the wings are folded) to give a total of nine wing regions for stimulation (see Fig. 6). A single bin was stimulated using a fine paintbrush in all ten animals sequentially, before a second bin was tested. Stimulus locations were tested in a pseudo-random sequence. When all bins had been stimulated once in all animals, the procedure was repeated another four times to give a total of N=450 stimulations. The start positions were then changed and the full stimulation protocol repeated (to give a total of N=900 stimulations). No individual animal was stimulated twice within 5 min. Half of the animals were initially tested in the anterior start position whereas the other half began in the posterior start position. We ensured that animals were standing still when the stimulus was given. Spontaneous scratching did not occur during an experiment in our setup. Behaviour was scored as either an ipsilateral or contralateral scratch (in accordance with behaviour described in Matheson, 1997, 1998) or as 'no scratch'. Since each animal was stimulated 5 times in each region (for each start position), the occurrence of a single scratch yielded a response probability of 20%. The likelihood of scratching therefore falls into six percentage categories (0%, 20%, 40%, 60%, 80%, 100%). Non-parametric (Kruskal–Wallis) analyses of these data were carried out using SPSS version 10 for Windows (SPSS Inc.) Data are presented as box plots in which coloured boxes represent the interquartile range and the bold line in each is the median value. Whiskers represent the full range of the data.

In a second stimulation experiment ten different animals were set up, using only the anterior start position. After the first block of 450 stimulations delivered as above, the exteroceptors on the postcubitus vein were ablated by cauterising the shafts of the long hairs and then covering the vein in a layer of low melting point beeswax. The animals were left overnight to recover, and the stimulation protocol was repeated on the following day.

In a third stimulation experiment to test the effectiveness of chemoreceptive sensilla in eliciting scratching, five different animals were set up without a start pole, so they stood with all of their tarsi on the foam ball. They were placed in a fume hood. A point half way along the wing of each animal was stimulated with a standard 0.2 ml puff of air delivered by hand through a blunt 21-gauge needle attached to a 1 ml syringe. In a second round of stimulations, the ipsilateral tarsus was stimulated in the same way. These two stimuli were alternated until each animal had experienced five stimulations of each site. The entire stimulation protocol was then repeated using 0.2 ml of acetic acid vapour drawn from the headspace of a flask containing glacial acetic acid (Rogers et al., 2003), delivered in the same way. Leg movements made in response to stimulation by either air or acetic acid vapour were scored as a scratch, an avoidance response or as a nil response. To prevent sensitisation or adaptation no animal was stimulated at any location more than once within 1 min.

Results

The focus of this paper is the trichoid hairs of the dorsal surface of the forewings because this is the surface that has been stimulated in most previous studies of scratching behaviour. We first describe our categorisation of hairs and describe their general distribution across both surfaces of both the forewings and hindwings. We then map in detail the locations of the different hair types on the dorsal surface of the forewings. Finally we relate these distributions to our ability to elicit scratching by activating receptors on different regions of the forewing.

Categories of trichoid hair

Hairs on the dorsal surface of the forewings fell into a clear trimodal distribution of lengths (Fig. 1A) and were thus classified into three types, which could also be distinguished on morphological and physiological grounds, as described below.

Short hairs ranged in length from 14–46 μm (N=16 hairs;

Fig. 1B,C). Each was set in a socket and stood perpendicular to the cuticle, with little curvature of the shaft. The short hairs had a pore at the tip (Fig. 1C) and were always multiply innervated (Fig. 2A). One of the sensory afferents in each sensillum responded to the initial mechanical stimulus of an electrode being placed over the hair shaft, or movements of the sensillum (Fig. 2A, lower trace), whereas one or more other afferents responded to the solution contained within the recording electrode (Fig. 2A, upper trace). These hairs are therefore basiconic sensilla (Kendall, 1970; Newland, 1998). We found no hairs of less than 14 μm on the dorsal surface of the forewings using either nailpolish casts or scanning electron microscopy. Basiconic sensilla were only found on the dorsal surface of the forewings (Fig. 2A) and the ventral surface of the hindwings (Fig. 2E), and were not found on the ventral surface of the forewings or the dorsal surface of the hindwings (Fig. 2). This distribution was consistent across all five animals examined.

Medium length trichoid hairs ranged from 73–159 μm in length on the upper surface of the forewings (N=17) and inserted into sockets that had a raised rim (Fig. 1D). Their shafts had slight curvature and tapered evenly from base to tip. Medium length hairs were found on dorsal and ventral surfaces of both forewings and hindwings, and were always singly innervated (Fig. 2C,D,F). Neither medium nor long hairs possessed a pore at the tip of the hair shaft so we could not obtain tip recordings from intact hairs. Recordings were always obtained from the cut shaft.

Long hairs ranged in length from 316–511 μm in 13 hairs and inserted into sockets that resembled those of the medium length hairs (Fig. 1F). Recordings revealed spikes of just one amplitude, elicited in response to movement of the hair shaft (Fig. 2B).

In addition to innervated hairs, the hindwing possesses many other hair-like structures on the wing veins and on the membrane of the anal region (Fig. 1G). They are of variable length

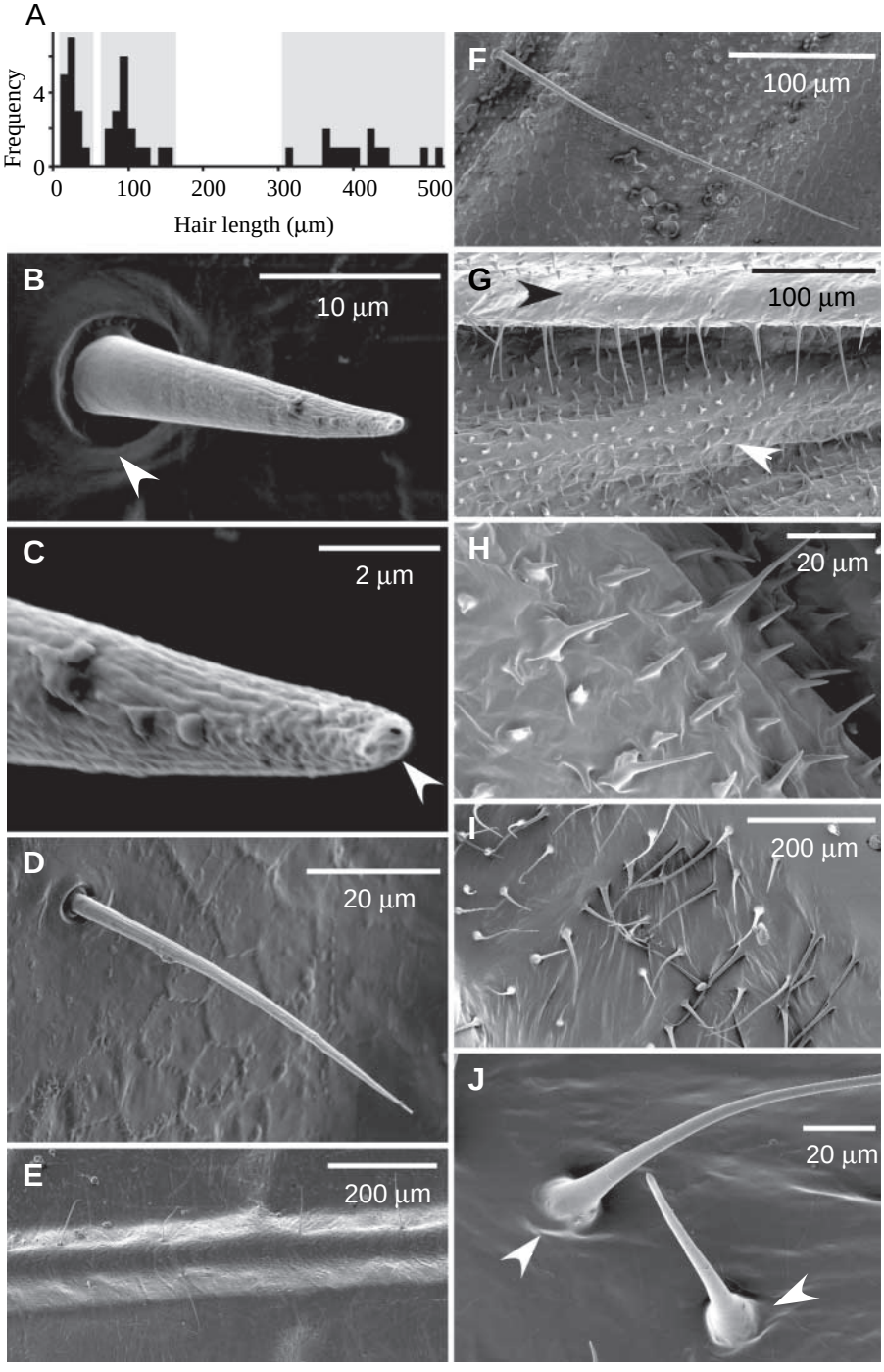

Fig. 1. Trichoid hair types present on the dorsal surfaces of the forewings of *Schistocerca gregaria*. (A) Distribution of hair lengths measured from SEMs. Grey boxes highlight the trimodal nature of the distribution. (B) Short hair with socket (arrowhead). (C) Enlargement of the pore at the tip of the shaft of the short hair shown in B (arrowhead). (D) Medium length hair with socket but no pore. (E) Medium length hairs on the subcosta vein point towards the leading and trailing edges at irregular intervals. The trailing edge is up, distal is to the right. (F) Long hair on the postcubitus vein, with socket but no pore. (G) A variety of hair-like structures on a wing vein (black arrowhead) and on the wing membrane (white arrowhead) of the hindwing anal region. (H) The shorter hair-like structures on the hindwings are variable in length and do not insert into a socket. (I) Longer hair-like structures on the proximal 10–15 mm of a forewing, near the wing's articulation with the thorax. (J) Enlargement of the long hair-like structures near a forewing's articulation. These longer structures do not have a socket (arrowheads) or a pore at the tip.

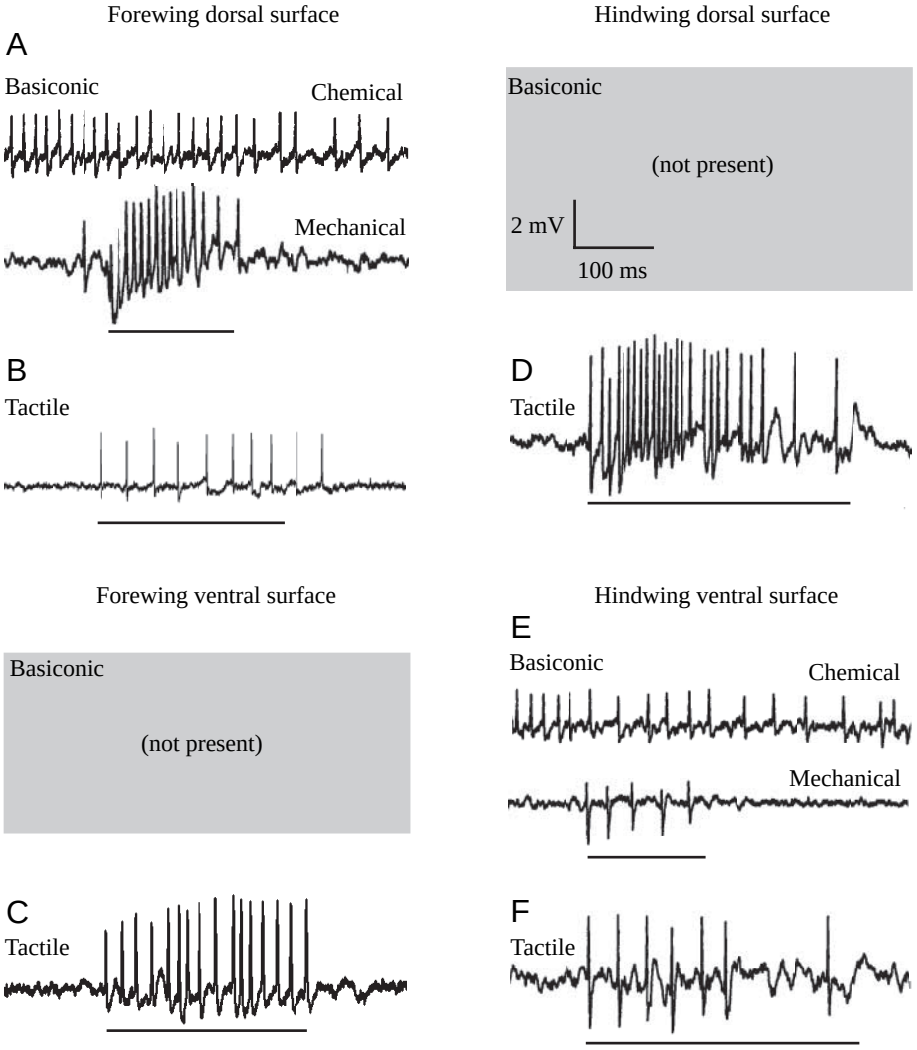

Fig. 2. Characterisation of trichoid hairs on the wings. (A) Two sections of a continuous recording from a basiconic sensillum on the dorsal surface of a forewing. One afferent responded with an 800 ms burst of spikes after the electrode was first placed over the intact tip of the sensillum (upper trace). After the afferent fell silent, a brief movement of the sensillum (horizontal bar) elicited a burst of spikes in a second afferent that had larger amplitude spikes (lower trace). (B) The afferent of a long hair on the postcubitus vein of the upper surface of a forewing responded with a burst of spikes to a brief movement of the hair (bar). The recording was made from the cut shaft. (C,D,F) Recordings from the cut shafts of medium length hairs on the ventral surface of a forewing (C), dorsal surface of a hindwing (D) and ventral surface of a hindwing (F). In all cases, movement (bars) elicited a burst of spikes in a single afferent. (E) Two sections of a continuous recording from a basiconic sensillum on the ventral surface of a hindwing. One afferent responded with a 600 ms burst of spikes after the electrode was first placed over the intact tip of the sensillum (upper trace). After the afferent fell silent, a brief movement of the sensillum (horizontal bar) elicited a burst of spikes in a second afferent that had a different waveform (lower trace). Basiconic sensilla were not seen on the ventral surface of the forewings or dorsal surface of the hindwings.

and do not have a socket (Fig. 1H). The proximal 10-15mm of both the forewings and hindwings, near their articulation with the thorax, are also densely covered with longer hair-like structures (Fig. 1I). These also do not have a socket or a pore at the tip (Fig. 1J) and we could never obtain recordings from the intact or cut shafts on either wing. They appeared less stiff than tactile hairs, so that mechanical stimuli bent the shaft rather than pivoting the hair about its base.

Locations of trichoid hairs on the dorsal surface of the forewings

The overall ratio of basiconic:medium:long hairs on the dorsal surface of the forewings was 4.8:2.0:1 in males and 3:2:1 in females. Basiconic sensilla were distributed on many principal and cross veins on the dorsal surface of the forewing (Fig. 3B,C). They were most densely packed on the costa and subcosta, which together possessed 49±2.7% (mean ± S.E.M., N=10) of the total number on the dorsal surface of the wing (males and females pooled). Only 8±2% were found on the postcubitus. The wings of male and female locusts differ in size, so comparisons between the sexes were based on the density of hairs rather than the absolute number. Across the whole wing surface, there was no significant difference in the density of basiconic sensilla between males and females (MANOVA, $F_{(1,56)}$=1.07, P=0.31) although there were differences between all the individual veins (MANOVA, interaction $F_{(6,56)}$=27.8, P=0, see Fig. 4A).

Medium length hairs were unevenly spaced on the costa, subcosta, radius and media (Fig. 3B,C). 88±5.2% of medium length hairs were found on the subcosta alone, with all other veins having lower densities (MANOVA, $F_{(6,56)}$=83.5, P<0.01). The spacing and orientation of medium length hairs on the subcosta are illustrated in Fig. 1E. They generally pointed towards either the leading or trailing edge of the wing. Females had a 1.5-fold greater density of medium length hairs on the subcosta (14.9±1.1 hairs cm^{-1}) than did males (9.7±1.7 hairs cm^{-1}: ANOVA, $F_{(1,8)}$=6.32, P<0.05, see Fig. 4B). Medium length hairs were more sparsely distributed on the ventral surface of the forewing, and on both surfaces of the hindwing.

Long hairs had the most restricted distribution, with 93±3.6% occurring on the postcubitus. An additional cluster of

hairs beyond the distal end of this vein were counted as wingtip hairs (Fig. 3B,C). Females had a 1.5-fold greater density of long hairs on the dorsal forewing postcubitus (8.1±0.2 hairs cm^{-1}) than did males (5.3±0.5 hairs cm^{-1}: MANOVA, $F_{(1,56)}$=29.37, P<0.01). This difference increased to twofold if hairs at the distal end of the postcubitus were included; see Fig. 4C).

When the forewing was extended laterally, as occurs during flight, the long hairs lay slanted towards the trailing edge of the wing. At rest, however, the wings are folded along the claval furrow, with the vannus of one forewing overlapping the other. The long hairs then stand up vertically so that they protrude above the animal (Fig. 5). In this position, the postcubitus veins of the two forewings present two parallel rows of long hairs along much of the length of the wings (Fig. 5B,C).

To relate the distribution of hairs to the probability of

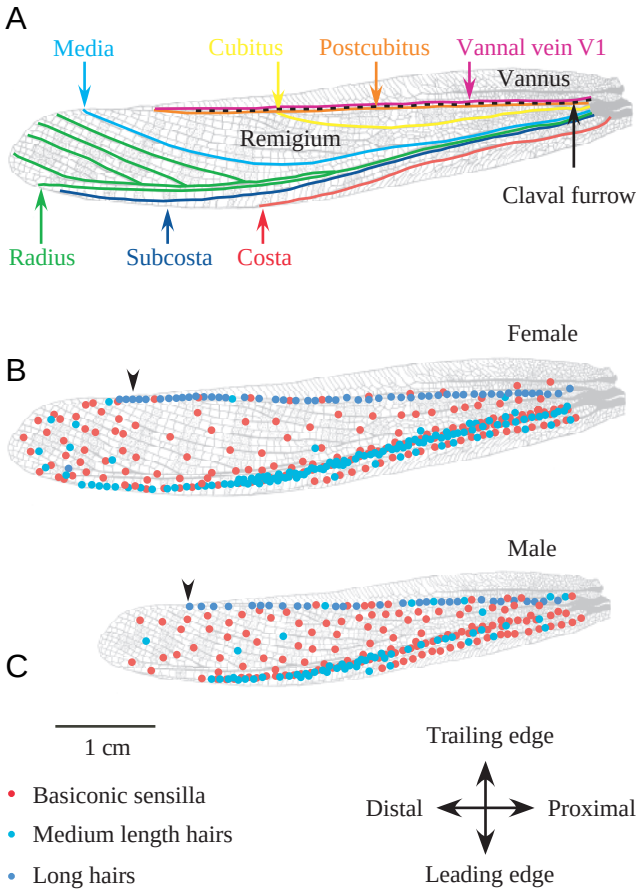

Fig. 3. Schematic representation of the average distribution of trichoid hairs on the dorsal surface of a locust forewing (based on N=5 detailed drawings). (A) The principal veins of the forewing, named according to Albrecht (1953). The vannus region of the trailing edge is delineated by the claval furrow (broken line) that lies between the postcubitus and vannal veins. The furrow forms a hinge so that at rest the vannus is folded over the dorsal surface of the animal, i.e. the vannus of one wing overlaps the vannus of the other (see Fig. 5A). (B,C) Average distribution of the three types of hairs on the forewings of female (B) and male (C) locusts. The total numbers were counted per vein in five animals and the mean numbers are indicated here (each colour-coded dot represents one hair). This representation does not reflect the exact locations of hairs in any one preparation. Basiconic sensilla occurred on many of the veins (red dots) whereas medium length hairs occurred in greatest numbers on the subcosta (light blue dots) and long hairs occurred only on the postcubitus (dark blue dots). Black arrowheads indicate long hairs that were counted as part of the wingtip region.

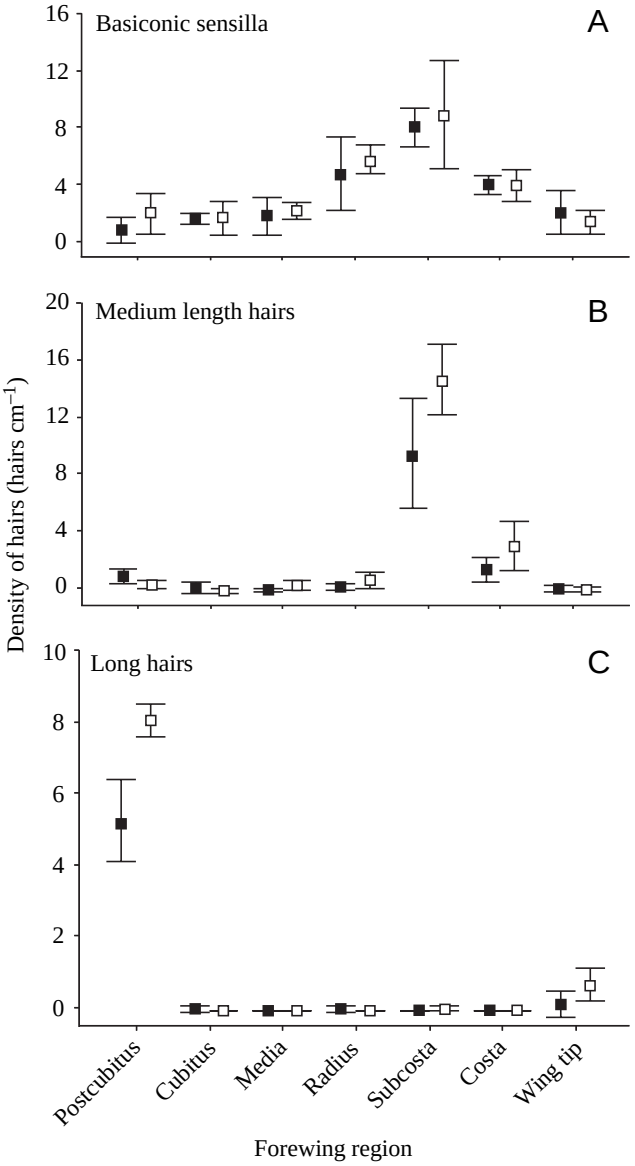

Fig. 4. The density of each of the three hair types on the principal veins of the dorsal surface of the forewings in male and female locusts. (A) Basiconic sensilla occurred on all of the veins but were most numerous on the subcosta. (B) Medium length hairs occurred primarily on the subcosta. (C) Long hairs were restricted to the postcubitus and wing tip. Values are means ± S.D., N=5 animals. There were no differences in the densities of basiconic sensilla on male and female forewings (A), but females had significantly more medium hairs on the subcosta than did males (B), and more long hairs on the postcubitus than did males (C). Filled squares, males; open squares, females.

eliciting scratching behaviour, we recounted the number of hairs in each of the nine regions used as stimulus sites in the behavioural analyses (Fig. 6C, and see Materials and methods).

The number of long hairs were evenly spaced, therefore the number of hairs per region did not differ significantly along the proximal–distal axis in trailing edge regions 1–4 (Fig. 6A, ANOVA, $F_{(3,36)}$=0.35, P=0.79).

The number of medium hairs per region differed significantly along the wing from regions 6–9 (Fig. 6B, ANOVA, $F_{(3,36)}$=4.30, P<0.05). The greatest number was in region 8 in both males (containing 35±2.1% of the total number of medium length hairs) and females (40±2.6%). The difference in the number of medium hairs between males and females also differed significantly along the length of the subcosta (ANOVA, $F_{(3,32)}$=3.51, P<0.05). The largest difference between the two sexes occurred in region 7, where females had a total of 26.2±2.1 and males 8.2±1.5 medium length hairs, which is a 3.2-fold difference between the sexes.

Probability of eliciting a scratch

Effect of gender

When standing in the anterior start position, females scratched ipsilaterally (scratch of the ipsilateral wing with the ipsilateral leg) in response to 60% of stimuli (interquartile range: 60%), whereas males scratched ipsilaterally in response to only 20% of stimuli (interquartile range: 60%). This difference is significant (Kruskal–Wallis test, χ^2=7.48, d.f. 1, P=0.006).

Effect of stimulus site

When standing in the anterior start position, the likelihood of eliciting a scratch differed significantly for stimuli applied to different regions of the forewing surface (Fig. 7, Kruskal–Wallis test, χ^2=24.51, P=0.002). Stimulation of trailing edge regions was most successful at eliciting scratching (Fig. 7A). Stimulation of these sites elicited a scratch on 20% of occasions (median, interquartile range 20%), whereas stimulation of leading edge regions (Fig. 7B) gave rise to a median likelihood of 0% (interquartile range 20%), both sexes pooled (Kruskal–Wallis test, χ^2=20.95, d.f. 1, P=0.000). There was no significant difference in the scratching probability of either sex along the anterio-posterior axis of the trailing edge regions 1–4 (males, Kruskal–Wallis test, χ^2=0.37, d.f. 3, P=0.78; females, Kruskal–Wallis test, χ^2=0.63, d.f. 3, P=0.61) or leading edge regions 6–9 (males, Kruskal–Wallis test, χ^2=0.50, d.f. 3, P=0.56; females, Kruskal–Wallis test, χ^2=0.72, d.f. 3, P=0.56).

Likelihood of eliciting a contralateral scratch

When standing in the anterior start position, stimulation of trailing edge regions was significantly less likely to elicit a contralateral scratch (scratch of the contralateral wing with the contralateral leg) than was stimulation of leading edge regions (Kruskal–Wallis test, χ^2=22.0, d.f. 1, P=0.000). Females scratched contralaterally in response to 20% of stimuli (interquartile range: 45%), whereas males scratched contralaterally in response to only 0% of stimuli (interquartile range: 20%) when data were summed across all wing regions (Kruskal–Wallis test, χ^2=4.81, d.f. 1, P=0.028).

Effect of hind leg start position

To determine the effect of start position we first pooled data from the two sexes. Start position had a significant effect on the overall likelihood that a touch on a wing elicited an ipsilateral scratch (Kruskal–Wallis test, χ^2=3.86, P=0.049). Locusts standing in the anterior start position (see Fig. 7C) had a 20% overall likelihood of scratching (median, interquartile range: 40%) whereas those standing in the posterior start position had a 0% overall median likelihood (interquartile range: 20%).

When the animal was standing in the posterior start position, females scratched ipsilaterally in response to 20% of stimuli (interquartile range: 20%), whereas males scratched ipsilaterally in response to 0% of stimuli (interquartile range:

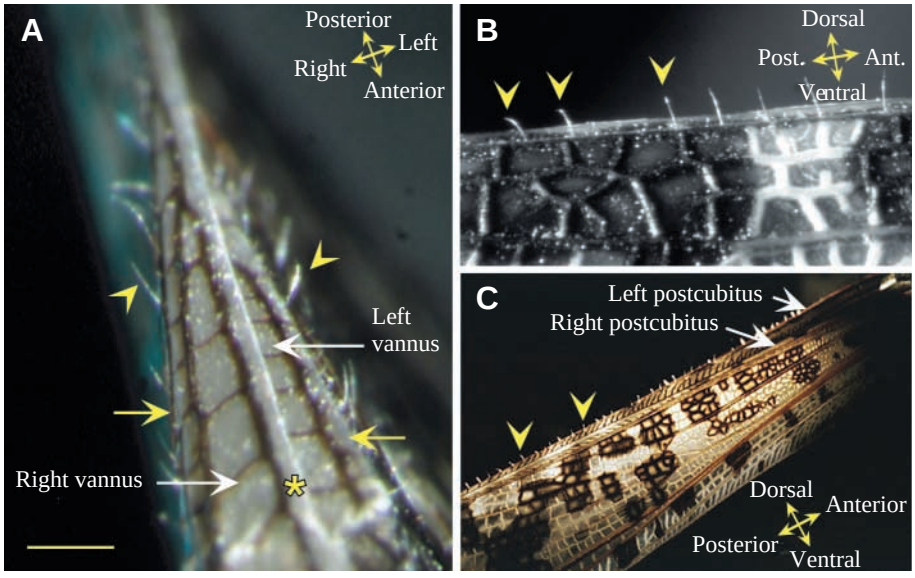

Fig. 5. (A) When the wings are folded, the vannus of one wing (here the right) folds over the other, bending at the claval furrow (yellow arrows). The asterisk indicates the trailing edge of the right wing. Long hairs on the postcubitus (e.g. arrowheads) stand up vertically above the animal's dorsal surface in two rows. (B) The long hairs point dorsally and slightly posteriorly. (C) The row of long hairs on the postcubitus of the left wing glint in the light, indicating clearly their length relative to the depth of the wing. Those on the right wing cannot be seen here because they are in shadow. Scale bar, 1 mm (A); 2 mm (B); 5 mm (C).

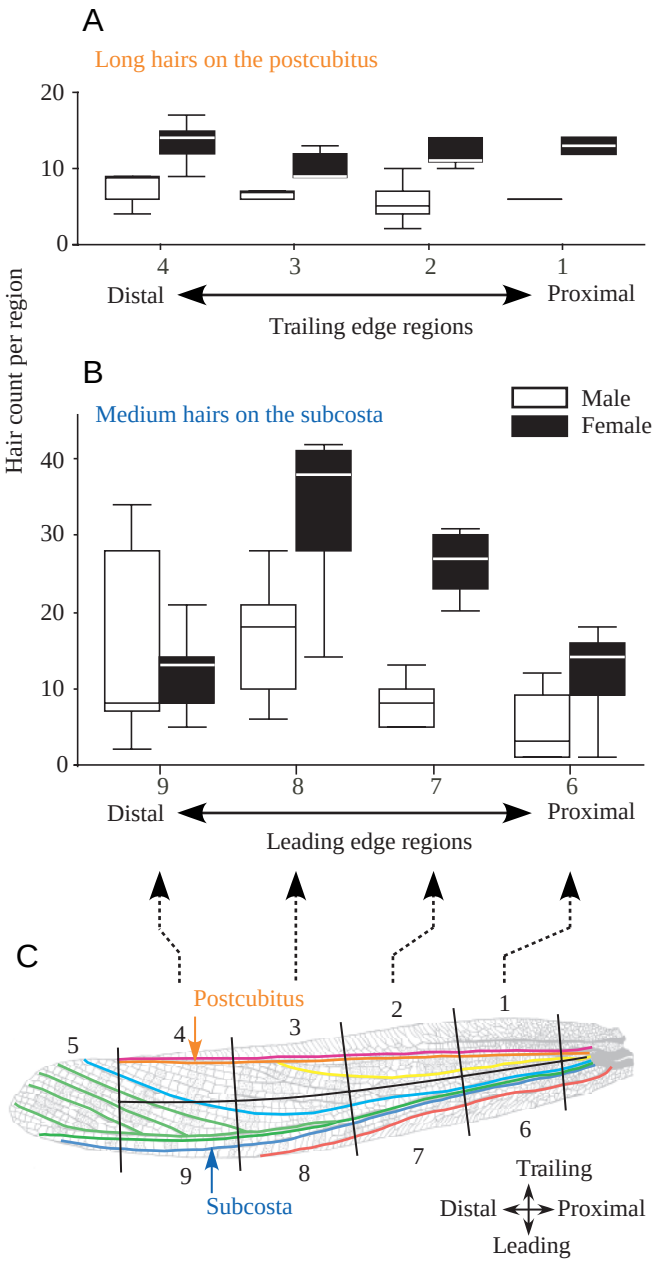

Fig. 6. Distribution of hairs within 9 stimulus regions. Medium length hairs occurred primarily on the subcosta (see Fig. 4), which runs through leading edge regions 6–9. Long hairs occurred primarily on the postcubitus (see Fig. 4), which runs through trailing edge regions 1–4. (C) Schematic representation of stimulus regions 1–9 and their relationship with the principal wing veins. (A) Long hairs on the postcubitus were distributed evenly across the trailing edge regions. Note that the region 4 included the cluster of long hairs at the distal end of the postcubitus. (B) The density of medium hairs on the subcosta was greatest in region 8. Females had more medium and long hairs than males in all regions (A,B). Boxes indicate the interquartile range, containing 50% of values, whiskers indicate the range, and horizontal lines within boxes indicate the median. Where there was no variability, only the median is shown as a horizontal line.

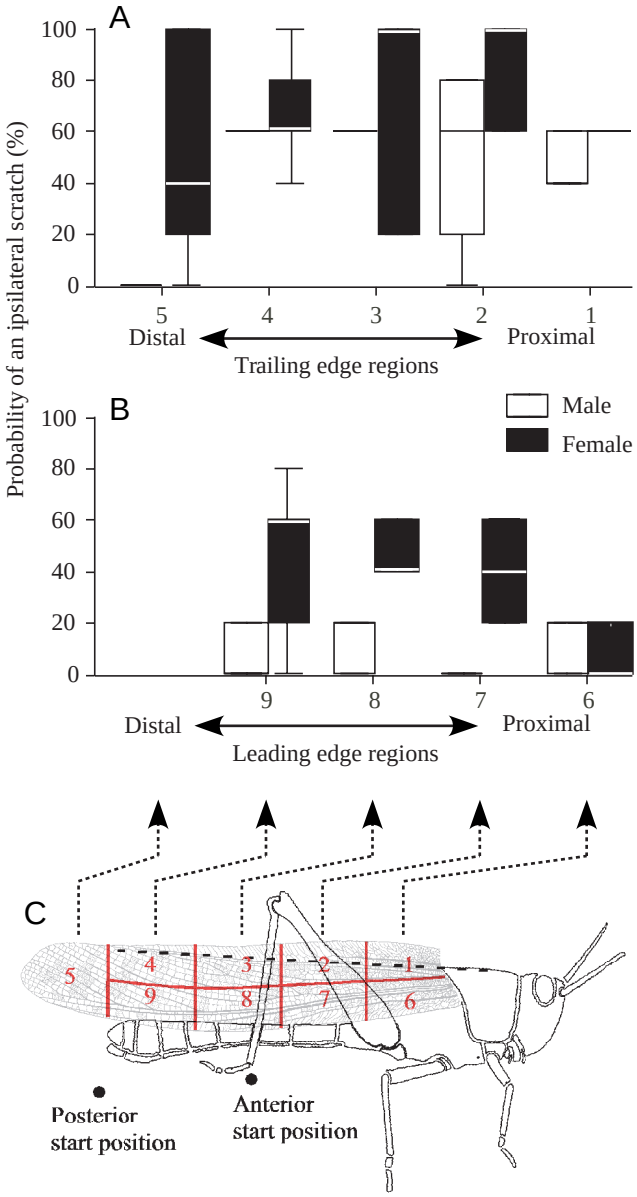

Fig. 7. The probability of eliciting an ipsilateral scratch differed when different regions on the dorsal surface of a forewing were stimulated. The probability of eliciting a scratch was generally higher for trailing edge regions 1–4 (A) than for leading edge regions 6–9 (B). Females had a higher likelihood of scratching than males for all regions except the wing tip (region 5; A, C). All of the scratches analysed started with the tarsus in the anterior start position (C). Wing regions are indicated with coloured numerals, and the claval furrow is indicated by a broken line. The vannal region of the wing above the claval furrow is normally folded across the dorsal surface of the body, but is shown here flattened out. Dotted arrows indicate corresponding wing regions in both histograms. Boxes indicate the interquartile range, containing 50% of values, whiskers indicate the range, and horizontal lines within boxes indicate the median. Where there was no variability, only the median is shown as a horizontal line.

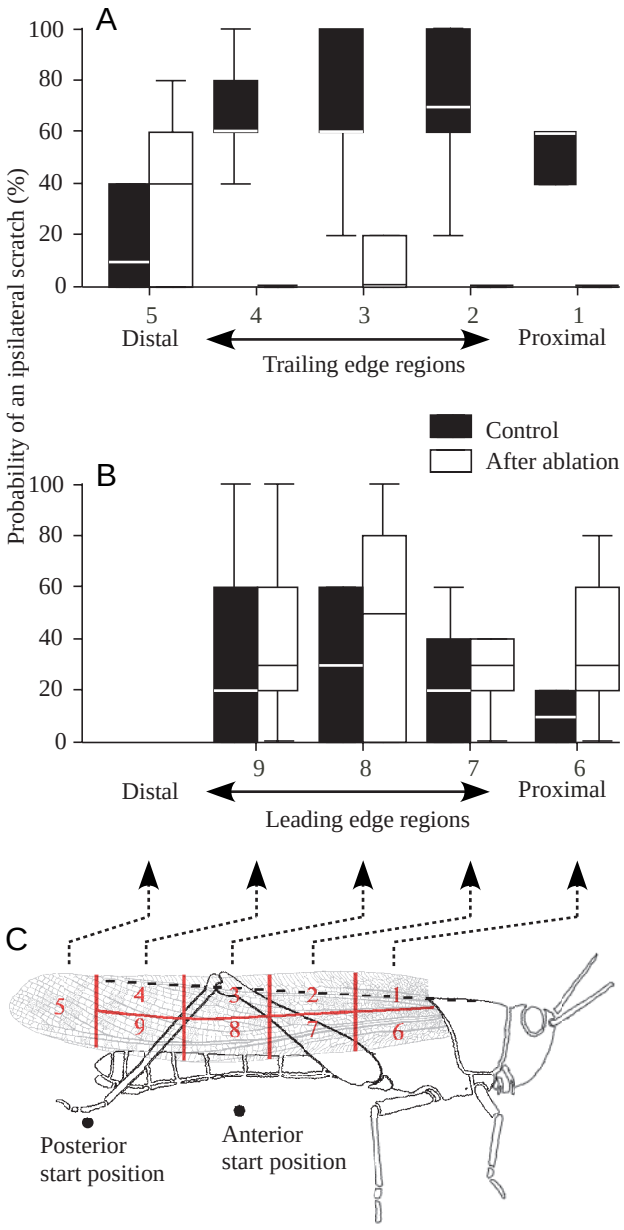

Fig. 8. Ablating long hairs on the postcubitus (in trailing edge regions 1–4) had a significant effect on the likelihood of eliciting a scratch when stimulating any of the regions 1–9. (A) Following ablation the probability of eliciting a scratch declined for the trailing edge regions 1–4, but increased for the wingtip region 5. (B) Following ablation the probability of eliciting a scratch increased for leading edge regions 6–9. (C). Wing regions are indicated with coloured numerals, and the claval furrow is indicated by a dashed line. The vannal region of the wing above the claval furrow is normally folded across the dorsal surface of the body, but is shown here flattened out. Dotted arrows indicate corresponding wing regions in both histograms. Boxes indicate the interquartile range, containing 50% of values, whiskers indicate the range, and horizontal lines within boxes indicate the median. Where there was no variability, only the median is shown as a horizontal line.

25%). This was not significant (Kruskal–Wallis test, χ^2=0.23, d.f. 1, P=0.630). Because of the low overall likelihood of eliciting scratches when animals stood in the posterior start position, we could not carry out a detailed analysis of the effect of stimulus site. Nevertheless, there was an overall effect of stimulus site (Kruskal–Wallis test, χ^2=17.05, d.f. 6, P=0.030), and the pattern of scratch probability across regions was similar to that for the anterior start position shown in Fig. 7 (data not shown).

Relationships between numbers of hairs and probability of eliciting a scratch

When data for both sexes were pooled there was a significant correlation between the number of medium length hairs in a region and the probability that stimulation of that region would elicit an ipsilateral scratch (Spearman's rank correlation test, ρ=0.307, P=0.027). When the sexes were analysed separately, there was no significant correlation between number of medium length hairs in a region and the probability of eliciting a scratch (Pearson's test, males: ρ=–0.112, P=0.43; females: ρ=–0.410, P=0.25). This lack of significance will in part be due to the low inter-animal variability in the number of hairs and the coarseness of the probability scale.

Due to uniform number of hairs per region (see 'Locations of trichoid hairs' above), there was no correlation between the number of long hairs in a region and the probability of eliciting an ipsilateral scratch (Pearson's correlation, r=0.220, P=0.173).

Ablation of exteroceptors

Ablation of long hairs on the postcubitus vein (which runs through trailing edge regions 1–4) had three main effects. First, it almost completely abolished responsiveness to touch in regions 1–4 in all animals (Fig. 8A), and therefore significantly reduced the overall probability of eliciting an ipsilateral scratch (Kruskal–Wallis test, χ^2=12.15, d.f. 1, P=0.000, both sexes pooled). Second, there was an increase in the sensitivity of leading edge regions 6–9 (Fig. 8B) and the wing tip region 5 (Fig. 8A) (Kruskal–Wallis test, χ^2=28.21, d.f. 1, P=0.000). Third, it significantly affected the likelihood of contralateral scratching (Kruskal–Wallis test, χ^2=14.70, d.f. 1, P=0.000). In control stimulations, contralateral scratching occurred more often in response to stimulation of leading edge regions than trailing edge ones. But following the ablation of hairs on the postcubitus, the probability of a contralateral response to stimulation of non-manipulated leading edge sites was reduced from 40% to 0% (interquartile range 40%). The probability of eliciting a contralateral scratch by stimulation of trailing edge regions 1–4 was not affected by ablation since median probability was 0% both before and after (interquartile range 40%).

Chemical odour stimulation of exteroceptors

Puffing the odour of acetic acid over the dorsal surface of a forewing was no more likely to elicit an ipsilateral scratch than was air (Kruskal–Wallis test, χ^2=1.48, d.f. 1, P=0.22) (Table 1). In contrast, puffing the odour of acetic acid over the

Table 1. *Responses of animals to puffs of acetic acid odour or air directed to either the wing or the hind leg tarsus*

	Scratch	Avoidance	No response
Wing			
Acetic acid	5 (10%)	0 (0%)	45 (90%)
Air	2 (4%)	0 (0%)	48 (96%)
Tarsus			
Acetic acid	0 (0%)	37 (74%)	13 (26%)
Air	2 (4%)	3 (6%)	45 (90%)

Tabulated values are the number of responses and percentage, pooled across N=5 animals.

tarsus of a hind leg was more likely to elicit an avoidance response of that leg than was an air-puff applied to the tarsus (Kruskal–Wallis test, χ^2=50.20, d.f. 1, P=0.000) (Table 1).

Puffing the odour of acetic acid over the tarsus of a hind leg was sevenfold more likely to elicit an ipsilateral hindleg avoidance response than was odour stimulation of the forewing likely to elicit an ipsilateral scratch (Table 1).

Discussion

We show that exteroceptive hairs of at least three types are distributed in characteristic patterns on the wings of *Schistocerca gregaria* (Figs 1–6). The longest hairs are almost exclusively restricted to the postcubitus vein of the forewings where they stand upright at rest, forming dorsal rows in an ideal position to detect contact from above. Touching the regions of the forewings where long hairs are located has a higher probability of eliciting a scratch than does touching other regions (Fig. 7), and ablation of the long hairs almost completely abolishes responsiveness to touch in the manipulated regions (Fig. 8). The odour of acetic acid detected by chemosensory afferents of basiconic receptors on the legs provides a powerful stimulus for leg withdrawal reflexes (as described previously by Newland, 1998), but when applied to the wing is no more effective than a puff of air in eliciting a scratch (Table 1).

Distribution of exteroceptors

The lengths of basiconic sensilla on the wings of the locust are similar to the range of lengths of basiconic sensilla on the hindleg tibiae (14–46 μm) (Burrows and Newland, 1994). They occur on all veins across the whole dorsal surface of the locust forewing, but not on the membrane between veins and cross veins. Female locusts have more basiconic sensilla on their forewings than do males, but also have larger wings; therefore the receptor density is the same in the two sexes. Basiconic sensilla are present only on the dorsal surface of the forewings and the ventral surface of the hindwings. This pattern of distribution makes sense for contact chemoreceptors, since the dorsal surfaces of the forewings are permanently exposed to the environment, whereas the ventral surfaces and the hindwings are protected at rest (Uvarov, 1966).

The comparative studies of Zaćhwilichowski in the 1930s described many multiply innervated sensilla, but such receptors were not recognised as being chemoreceptors (basiconic sensilla) (Zaćhwilichowski, 1934a,b, 1936). In locusts too, multiply innervated hairs of approximately 40 μm in length were described (Knyazeva, 1934, 1970), but again were not shown to be chemosensory. Few studies have explicitly recognised the presence and location of chemoreceptors on the insect wing (Angioy, 1981; Pietra, 1980; Dickinson, 1997).

Hairs longer than 40 μm have not previously been described on the surface of locust forewings (Knyazeva, 1970). We can find no report of hairs longer than 200 μm on the forewing surface of any orthopteran species, although such long hairs are found on the wing's articulation with the thorax (Knyazeva, 1970). Trichoid hairs on the hindlegs range from 60–780 μm (Newland, 1991) and there are long filiform hairs on the prosternum (500–600 μm; Pflüger and Tautz, 1982), head (up to 300 μm; Weis-Fogh, 1949) and cerci (20–500 μm; Thomas, 1965).

We show that the distributions of medium (73–159 μm) and long (316–511 μm) hairs on the forewings of *Schistocerca gregaria* are very similar to that described for the shorter hairs on the forewing of the grasshopper *Melanoplus sanguinipes* (Albert, 1976). In both cases the longest hairs (approximately 100 μm in *M. sanguinipes*) are restricted to the vein delineating the trailing edge, whereas the medium length hairs are most numerous on the veins supporting the leading edge. Note that the key figure (fig. 26) in Albert (1976) incorrectly labels the orientation of the wing, and mislabels the veins. Long hairs are far less numerous on the locust forewing than are medium length or short hairs, but the reverse is true of *M. sanguinipes*. Overall *M. sanguinipes* has many more tactile hairs than *Schistocerca gregaria*, even though it is approximately half the size.

Locust forewings have far fewer long and medium length hairs than do the larger hindwings. On a single hindwing there are approximately 12 400 hairs and bristles, 1160 of which are on the principal veins (Altman, 1978). Many of the hair-like structures lying on the membranous anal region of the hindwing are not innervated.

Scratching probability and tactile hair densities

The overall probability of eliciting scratching behaviour by touching a small region of a forewing is low. Using stimuli that cover a larger region, or that last for longer, can increase the probability (data not shown). For foreleg grooming of the sternum, isolation of the prothoracic ganglion increases the likelihood of eliciting the behaviour from virtually 0% to over 95% likelihood (Rowell, 1969).

Stimulating trailing edge regions of a forewing is significantly more likely to elicit scratching behaviour than is stimulation of leading edge regions. The principal vein present in this area is the postcubitus, which is covered in regularly spaced, long tactile hairs. Each of the four trailing edge regions (1–4) contains the same number of long hairs, and locusts are

equally likely to scratch in response to stimulation of any of them.

In the leading edge regions 6–9, most hairs occur on the subcosta. They are all short or medium length hairs. Across the sexes, there is a correlation between the number of medium length hairs per region and the probability of eliciting a scratch. The small variation in the number of hairs per region and the relative coarseness of the probability scale (five probability bins) meant that we could not demonstrate whether this correlation also holds within each sex.

The position of the ipsilateral hindleg at the start of stimulation also has a significant effect on the overall likelihood of scratching in response to stimulation of the forewing's dorsal surface. This suggests that proprioceptive inputs signalling the posture of the hindleg must impinge onto the local neuronal circuits that generate the aimed scratching movements. Such convergence of hindleg proprioceptive inputs and forewing exteroceptive inputs onto local and intersegmental interneurones has been demonstrated by Matheson (2002), providing the opportunity now to analyse how these two types of sensory information interact in the generation of an aimed movement.

Gender-specific differences

The forewings of female locusts have more medium length hairs on the subcosta, and more long hairs on the postcubitus, than do those of male locusts, and these differences are greater than predicted by the difference in wing size. In contrast most sexual dimorphisms in sensilla numbers observed in other insects species are related to differences in body size (Chapman, 1982). Exceptions to this rule occur mainly on the antennae of species that demonstrate sex-specific differences in feeding habits or pheromone detection (Chapman, 1982; Linardi and Chiarini-Garcia, 2002). Sexual dimorphism in hair numbers has not previously been described in locusts. The sexual dimorphism that we describe is positively correlated with the likelihood of eliciting a scratch (see previous section). Solitarious phase locusts have more olfactory sensilla on their antennae and more mechanosensory sensilla on their legs than do gregarious phase animals and these differences may be related to differences in the behaviours of solitarious and gregarious animals (Greenwood and Chapman, 1984; Ochieng, 1998; Rogers et al., 2000). Solitarious locusts groom spontaneously less frequently than do gregarious locusts (Simpson et al., 1999), but there has been no systematic study of either wing hair distributions or the strengths of sensory synapses in the two phases. Rearing conditions can also affect receptor numbers in locusts (Rogers and Simpson, 1997), but this could not have contributed to the differences that we describe, as all the locusts were reared together. The gender-specific difference in sensilla number is consistent with the difference in the probability with which a stimulus elicits a scratch. In the trailing edge regions where females possess twice as many long hairs as do males, females are 1.5-fold more likely to scratch in response to tactile hair stimulation. It is not known if the form of a scratching movement differs between males and females (Dürr and Matheson, 2003), but the difference in hair density raises the possibility that females could aim their movements more precisely if the target is encoded in a more finely grained sensory representation.

Function of exteroceptors

Mechanosensory afferents from basiconic sensilla on the legs are more sensitive to touch than are those of tactile hairs, and they are therefore effective at signalling very close contact with food, obstacles or conspecifics (Newland and Burrows, 1994; Rogers and Newland, 2003). Individual basiconic sensilla on the hindleg tibia are capable of eliciting spikes in spiking local interneurones (Burrows and Newland, 1994). Basiconic sensilla on the fore- and hindwings presumably enable the animal to respond to both mechanical stimuli and to chemicals brought into contact with the wing cuticle. These sensilla are the most numerous of the three hair types on the forewing dorsal surface and must represent an important form of mechanosensory input from the wing surface. The highest densities of basiconic sensilla are on the subcosta and costa, but mechanical stimulation of these leading edge regions has a lower probability of eliciting a scratch than stimulating the trailing edge regions where basiconic sensilla are sparsely distributed. We conclude that the mechanosensory afferents of basiconic sensilla have a weaker input to the networks underlying scratching than do those of the long hair afferents.

Both mechanosensory and chemosensory afferents from basiconic sensilla on the mesothoracic leg project somatotopically within the mesothoracic ganglion (Newland et al., 2000). Their projections overlap considerably with the arborisations of mechanosensory afferents from tactile hairs on corresponding regions of the leg (Burrows and Newland, 1994), suggesting that chemosensory information might be processed together with mechanosensory information within the CNS. Stimulation of basiconic sensilla on the forewing with a weak solution of acetic acid can elicit a reliable hindleg targeted scratching movement (K.P., personal observation). The odour of acetic acid alone can elicit 'leg-waving' behaviour in grasshoppers (Slifer, 1954; Slifer and Finlayson, 1956; White and Chapman, 1990) and a leg avoidance reflex in locusts (Newland, 1998). In contrast to this stimulation of the tarsus, acetic acid odour puffed over a forewing is no more successful at eliciting a scratch than is a puff of air. This may result from a higher threshold of response for wing chemoreceptors compared to leg chemoreceptors, or may indicate a more fundamental difference in the way that the information from the two surfaces is processed.

Ablating the long trichoid hairs on the postcubitus vein of a forewing reduces the high sensitivity of the trailing edge regions through which this vein runs. This manipulation also removed the few basiconic sensilla on this vein although all others, including those on the nearby cross veins, remained intact. The striking reduction in responsiveness of trailing edge regions following hair ablation clearly points to a role of the long hairs in eliciting a scratch. These hairs are the least numerous of the three types, and yet are highly effective at

eliciting scratching behaviour. At rest, the dorsal position of the long hairs, combined with their vertical orientation, make them well suited to detecting predators or conspecifics approaching from above. This may be particularly relevant to female locusts, since these hairs would be deflected by the thorax and abdomen of male locusts during both the precopulatory passive phase and copulation, which can last for several hours (Uvarov, 1966, Parker et al., 1974). Stimulation of regions that do not contain long hairs can also elicit aimed scratching, albeit with a lower likelihood. Basiconic sensilla and medium length hair sensilla presumably contribute to this drive. All hair types, therefore, could be stimulated by the presence of foreign material or parasites on the wing, which may be removed by scratching.

Our findings suggest that mechanosensory afferents from hairs on the forewings (which are mesothoracic appendages) provide an important input to metathoracic networks that drive hindleg scratching (Berkowitz and Laurent, 1996a,b; Matheson, 1997). In this context, forewing hairs function much like tactile hairs on the legs, stimulation of which can initiate local leg reflexes in which the hindleg is lifted away from the site of stimulation by the coordinated action of several leg joints (Burrows, 1996). These leg avoidance reflexes are computed locally, and involve movement of the stimulated appendage, whereas scratching movements made in response to stimulation of forewing hairs are computed intersegmentally. Scratches involve movement of one appendage (the hind leg) towards a target on another appendage (the wing) in a cyclical and often repetitious movement, which can outlast the duration of the stimulus. When the stimulus is prolonged or moves along the wing, locusts re-aim their leg movements appropriately (Matheson, 1998), indicating that forewing tactile hairs provide continuous feedback throughout the movement. Whether leg hairs that trigger leg avoidance reflexes can also provide ongoing feedback to modify those movements is unknown.

Scratches that are aimed at different locations on a wing necessarily differ in detail from one another, but there is no evidence that different forms of scratching are used to reach different locations on the forewing, and the behavioural responses thus form a continuum (Dürr and Matheson, 2003). Leg reflexes, in contrast, fall into discrete categories depending on the region of the hindleg being stimulated, and these categories can be related to distinct boundaries between the receptive fields of interneurones that receive inputs from the tactile hair afferents (Siegler, 1986). For scratching movements, hindleg proprioceptive inputs modulate both the initial outward trajectory and the overall accuracy (Dürr and Matheson, 2003). We show that the overall probability of eliciting a scratch differs for different start positions, so leg proprioceptive inputs may also modulate the overall gain of wing mechanosensory pathways. Moreover, since the kinematics of a scratch depend on start position (Dürr and Matheson, 2003), it is likely that the effective somatosensory receptive fields of interneurones and motor neurones driving scratching are modulated by leg proprioceptive inputs. At least one class of metathoracic local interneurone is strongly excited by both wing exteroceptive inputs and hind leg proprioceptive inputs (Matheson, 2002), but the detailed interactions between the two modalities within such neurones remain to be elucidated.

Previous papers describing wing tactile hairs have proposed that they are directional detectors of air pressure or wind velocity during flight (Knyazeva, 1970; Albert, 1976; Altman, 1978), but there is no direct evidence for such roles. Recordings of hindwing nerve 1A during flight reveal that many neurones fire in response to wing movements, but many of these are afferents from campaniform sensilla and it is not known if any of the remainder are afferents from tactile hairs (Wilson, 1961; Gettrup, 1965, 1966). We have shown that locust forewing hairs respond to chemical and mechanical stimuli when the locust is at rest and are responsible for eliciting hindleg scratching movements.

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