

Ontogeny of air-motion sensing in cricket

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Accepted 10 August 2006

Summary

Juvenile crickets suffer high rates of mortality by natural predators that they can detect using extremely sensitive air-sensing filiform hairs located on their cerci. Although a huge amount of knowledge has accumulated on the physiology, the neurobiology and the biomechanics of this sensory system in adults, the morphological and functional aspects of air sensing have not been as well studied in earlier life history stages. Using scanning electronic microscopy, we performed a survey of all cercal filiform hairs in seven instars of the wood cricket (*Nemobius sylvestris*). Statistical analyses allowed us to quantify profound changes in the number, the length and the distribution of cercal hairs during development. Of particular importance, we found a fivefold increase in hair number and the development of a bimodal length–frequency distribution of cercal hairs from the

second instar onwards. Based on theoretical estimations of filiform hair population coding, we found that the cercal system is functional for a wide range of frequencies of biologically relevant oscillatory flows, even from the first instar. As the cricket develops, the overall sensitivity of the cercal system increases as a result of the appearance of new hairs, but the value of the best tuned frequency remains fixed between 150 and 180 Hz after the second instar. These frequencies nicely match those emitted by natural flying predators, suggesting that the development of the cercal array of hairs may have evolved in response to such signals.

Key words: European wood cricket, functional morphology, mechanoreception, population coding model, sensory development.

Introduction

Sensory systems play an influential role in the ecology and behaviour of animals, and their structure, physiology and biomechanics show adaptations to both the intensity and quality of environmental signals (Dusenbery, 1992). Given that resource consumption and predation risk are generally related to body size, many species undergo significant shifts in food or habitat use as they grow (Werner and Gilliam, 1984; Heming, 2003) and show substantial commensurate developmental adjustment of their sensory equipment. Shift in sensitivity and signal coding during ontogeny has been recorded in a variety of taxa and senses including anuran and fish vision (Jaeger and Hailman, 1976; Job and Shand, 2001), mammal olfaction (Doty et al., 1984), mammal and fish hearing (Rubel, 1984; Kenyon, 1996) and fish electroreception (Denizot et al., 1998). In particular, sensors involved in the detection of predators represent interesting models in which to examine the functional consequences of change in sensory morphology during development. Juvenile stages generally suffer high rates of predation and their sensory systems, although often reduced, must provide the necessary information about the approaching predator to judge whether to respond and at what moment.

Thus, ontogenetic changes in sensory morphology may be expected to have important consequences for susceptibility to predatory attack and, hence, survival.

Among anti-predator sensory systems, the air-current-sensitive cercal system of orthopteroids (cricket and cockroaches) is one of the most sensitive in the animal kingdom (Shimozawa et al., 2003). These insects bear on their cerci hundreds of mechanoreceptive filiform hairs that respond to the faintest air movements, down to 0.03 mm s^{-1} (Shimozawa et al., 2003). Hair deflection produces a mechanical stress in the cercal afferent neuron under the hair base. The extreme sensitivity of the cricket's wind-detecting system allows the use of air flow patterns for early detection of flying predators, even at relatively large distances [up to 30 times their body length (Gnatzy and Heußlein, 1986)]. The hundreds of filiform hairs of varying lengths composing the cercal array of hairs and their associated neurons can encode the acceleration, the frequency and the direction of predatory air signals, providing the necessary information for the cricket to escape efficiently. Although a substantial amount of knowledge has accumulated on the physiology, the neurobiology and the biomechanics of this sensory system in adults (e.g. Camhi, 1984; Gnatzy, 1996;

Shimozawa et al., 2003), the morphological and functional aspects of air sensing have not been as well studied for earlier life history stages. Because most predation events do occur in early instars (Dangles et al., 2006a), studies that focus on juveniles are crucial to better understand the ecological significance of wind sensors throughout the development of these insects.

Events leading up to the development of sensory function include the simultaneous maturation of many neural and mechanical properties. In crickets, the increase in hair length during postembryonic development generates changes in coding properties of air velocity and acceleration by afferent neurons (Chiba et al., 1988). By contrast, the biomechanics of filiform hairs shows no clear changes either in terms of threshold angles or oscillation properties (Kanou et al., 1988; Kämper, 1992). More obviously, the cercal system of crickets undergoes important changes in number and length of filiform hairs as the cricket grows (Kanou et al., 1988) (O.D., personal observations). Surprisingly, no studies have ever quantified these changes and few have investigated the implications for cricket sensitivity to air currents (e.g. Chiba et al., 1988). The aim of the present study is to document how air current sensitivity changes as the full complement of receptors develops. We first quantified, precisely and exhaustively, changes in number, length and spatial arrangement of hairs over the surface of the cercus as a cricket grows. Second, we investigated the functional implications of these morphological changes by modelling the tuning efficiency of each instar submitted to biologically relevant oscillatory air signals by natural predators.

Material and methods

Wood cricket life cycle

The wood cricket (*N. sylvestris* Bosc 1792) is the dominant cricket in Western Europe where it lives in a wide range of habitats, including forests, grasslands and moorlands. These small crickets (7–10 mm in body length) are common on deciduous forest floors, reaching locally and temporally high densities up to 400 individuals m⁻² (Gabbutt, 1959a). The wood cricket life cycle consists of one generation every second year with diapause in both eggs and juveniles stage during winter (Gabbutt, 1959b). Their development comprises eight larval instars and one adult instar. The larval development

begins in June and early July with the first instar and successive instars occur until November when the insect over-winters as the fifth or occasionally the sixth instar. Growth starts again the following March and the sixth, seventh and eighth instars are present in the following two months until the adults finally appear in June or July (Gabbutt, 1959b).

Cricket sampling

Juvenile and adult male and female wood crickets were collected from ground litter on several occasions (spring, summer and autumn 2004) in a mixed deciduous forest nearby Tours (Larçay forest, 49°01'50"N, 06°05'52"E). Crickets were placed in 70° alcohol and returned to the laboratory. Following the method of Campan (Campan, 1965), instars were determined by measuring the tibia length of the posterior legs using a micrometer mounted on a stereomicroscope (Leica, MZ 13, Wetzlar, Germany). Seven instars out of nine were selected for this study: instar I, II, III, V, VI, VII and adult (Ad).

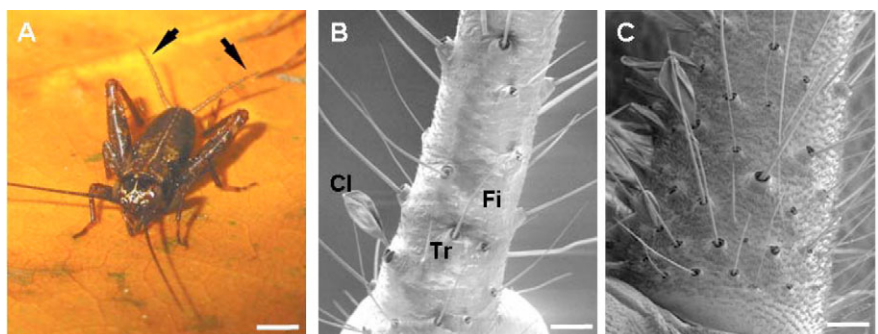
Cercus scanning

The hair array structure was examined by scanning electron microscopy (SEM, DSM 982 GEMINI, LEO Microscopie, Cambridge, England) of cerci that had been dissected from crickets, dehydrated and sputter coated with platinum. To perform a complete survey of wind sensitive hairs inserted on the three-dimensional conical surface of the cercus (see Fig. 1), we built a rotating stage which allowed us to take images from different angles under the microscope. For each instar, we took a set of five SEM images, from the base to the tip of the cercus, at eight different angles (0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°). Ten additional images at lower magnification (×40) were taken to measure the length of long filiform hairs (see below). In total, 50 SEM pictures were taken for each instar, and for technical reasons, replication was performed for only three instars (I, III, and Ad). We found weak inter-individual variability (<5%) in the structure of the cercal hair array, confirming previous studies on the cercal sensory system of crickets (Dangles et al., 2005; Magal et al., 2006). We observed no differences between left and right cerci (O.D., F.V., D.P. and J.C., unpublished data).

Morphological measurements on cerci

In addition to cercus length, three types of measurements were

Fig. 1. (A) Photographs of the wood cricket (*Nemobius sylvestris*) showing the location of the cercal sensory system at the end of the abdomen (black arrows); Scale bar, 2 mm. (B,C) Scanning electron microscopy images illustrating the change in cercal receptors size and number throughout development in *N. sylvestris*: (B) first instar; Scale bar, 20 µm; (C) adult; Scale bar, 100 µm. Images are of the basal region of the left cercus. Cl, clavate hairs; Tr, trichoid hairs; Fi, filiform hairs.



performed on cercus images from each instar. First, we counted all filiform hairs and calculated their overall density assuming that the cercus has a conical shape. As complementary measurements, we also counted the number of two other types of cercal receptors, the clavate and trichoid hairs, which are reported to be involved in the perception of gravity and touch (Edwards and Palka, 1974), respectively (see Fig. 1). Second, we calculated the three-dimensional coordinates of each filiform hair over the cercus. These data about hair positioning allowed us to investigate modifications in the spatial arrangement of receptors throughout cricket development (see Statistical analyses). Third, we measured the base diameter of each filiform hair on SEM pictures using Scion Image for Windows (Scion Corporation, Frederick, MD, USA). The base diameter (d) allowed us to estimate with precision the length of the hair (L) as there is an allometric relationship, $L=ad^b$, between these two variables (Kumagai et al., 1998; Magal et al., 2006). We calculated a and b parameters for each cricket instar, based on simultaneous measurements of base diameter and length for a series of 40 hairs of varying lengths perfectly located in the image plane.

Statistical analyses

We used the pair correlation function $G(r)$ (Ripley, 1981) to analyse the arrangement of cercal filiform hairs for each cricket instars. Following guidelines (Apanasovich et al., 2003), the conical point pattern of hairs over the cercus was cut lengthwise into two pieces corresponding to the lateral and the medial surfaces of the cercus. Owing to the presence of aggregated clavate hairs the basal part of the cercus was not considered for spatial analyses. The distribution pattern (random, aggregated or regular) of filiform hairs was evaluated by comparing the observed data with the null model of complete spatial randomness (for details, see Ripley, 1981). All spatial analyses were performed using the 'Spatial Stat' package of R software (R Development Core Team).

Frequency distributions of hair length were decomposed into Gaussian distributions using a combination of a Newton-type method and expectation maximization algorithms. Mean (μ_n), variance (σ_n), and proportion (π_n), for each n component distributions were calculated using the 'mixture distribution' package of R software (R Development Core Team). A χ^2 function was used for parameter estimations and goodness-of-fit testing when adjusting curves to histograms.

Modelling the sensitivity response of crickets to air signals

We used a mathematical model (Magal et al., 2006) to predict the consequences of ontogenetic changes in the cercal hair array structure for cricket sensitivity to air signals. This model combines the biomechanics of hair movement, the distribution of hair length in the entire array, and the relationship between single hair movement and its neurophysiological activity to predict the overall response of the cercal array to air signals of various intensities and frequencies. Briefly, an additive population coding of sinusoid signals of varying frequencies and velocities, taking into account hair directionality, produced the cercal array tuning curve. The proportions of each category

of directionality were supposed constant through development. The neurophysiological activity was implemented using the relationship between frequency and triggering velocity threshold values for each hair length (for details, see Magal et al., 2006). Hair number and the variation of hair length are key features of the cercal system of crickets as they fractionate both the intensity and the frequency range of an air stimulus. Longer hairs have their peak response at low frequency, whereas shorter hairs have a flat response over most of the frequency range, with a peak response at high frequency. The output of the model, the canopy response (CR, in radians), is the sum of the maximal hair deflection in the array of hairs.

In spite of the growth of filiform hairs throughout development, their threshold angle remains unchanged for a given hair length (Kanou et al., 1988). This property allowed us to estimate theoretically the sensitivity of the cercal array during cricket development by implementing the model with the hair length distributions measured for each cricket instar. We thereby obtained for each instar the cercal canopy response as a function of frequency (0–300 Hz) and intensity (0.05–5.0 cm s⁻¹) of biologically relevant oscillatory air signals from natural predators (see Gnatzy, 1996; Dangles et al., 2005).

Results

Structure of the cercal array throughout development

All types of hairs are present from the first instar of wood crickets. At this stage, the cercal hair array consists of 60 filiform hairs, two clavate hairs and four trichoid hairs (Table 1). The number of hairs on each cercus progressively increases with each moult to reach 322 filiform hairs, 51 clavate hairs and 395 trichoid hairs in the adult. The increase in filiform hair number is however not linear throughout development. We found a higher rate of increase during the two first moults than during later moults. Surprisingly, when taking into account the increase in cercus surface as crickets get larger, we found that the density of filiform hairs linearly decreases throughout development, from 436 hairs mm⁻² in the first instar down to 136 hairs mm⁻² in the adult (Fig. 2).

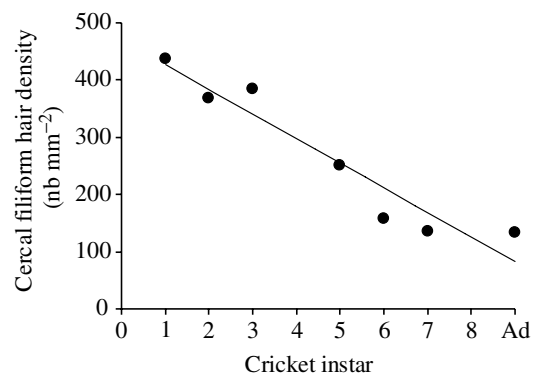


Fig. 2. Relationship between the density of filiform hair receptors and the instar of *N. sylvestris*. Linear regression: $y=-43.0x+469.3$; $r^2=0.91$, Spearman's $P<0.001$.

Table 1. *Cercus length, abundance of cercal receptors (clavate, trichoid and filiform hairs), and parameters of filiform hair length–frequency additive normal distributions at different instars of cricket development*

	Cricket instars						
	I	II	III	V	VI	VII	Adult
Cercus length (mm)	0.82	1.03	1.23	2.12	2.61	3.07	4.50
Total number of clavate hairs	2	5	12	25	30	39	51
Total number of trichoid hairs	4	24	55	200	231	264	395
Total number of filiform hairs	60	105	150	183	199	231	322
Mixture distributions of filiform hair length frequency							
μ_1 (μm)	191	143	194	132	103	113	170
σ_1 (μm)	113	102	100	110	102	65	84
π_1	1	0.79	0.77	0.81	0.81	0.77	0.82
μ_2 (μm)	–	504	542	578	599	633	730
σ_2 (μm)	–	90	92	103	130	163	172
π_2	–	0.21	0.23	0.19	0.19	0.23	0.18
χ^2_5	0.56	1.39	4.17	1.54	2.09	4.64	2.96
P	0.97	0.92	0.52	0.91	0.83	0.46	0.71

μ_n is the mean, σ_n the variance, and π_n the proportion of filiform hairs for each of the n distributions making up the mixture distribution. After the first moult, all crickets show a bimodal mixture distribution. Parameter estimations and goodness-of-fit are given by the χ^2 and P values.

Not only are more filiform hairs added to the surface of cerci during each successive moult of the cricket but existing filiform hairs increase in length. In the first instar, the hairs vary in length from 33 μm to 407 μm and their length distribution

presents a unimodal normal shape with a mean value of 191 μm and a variance of 113 μm (Fig. 3, Table 1). A bimodality of the hair length distribution appears from the second instar onwards, clearly separating hairs into two

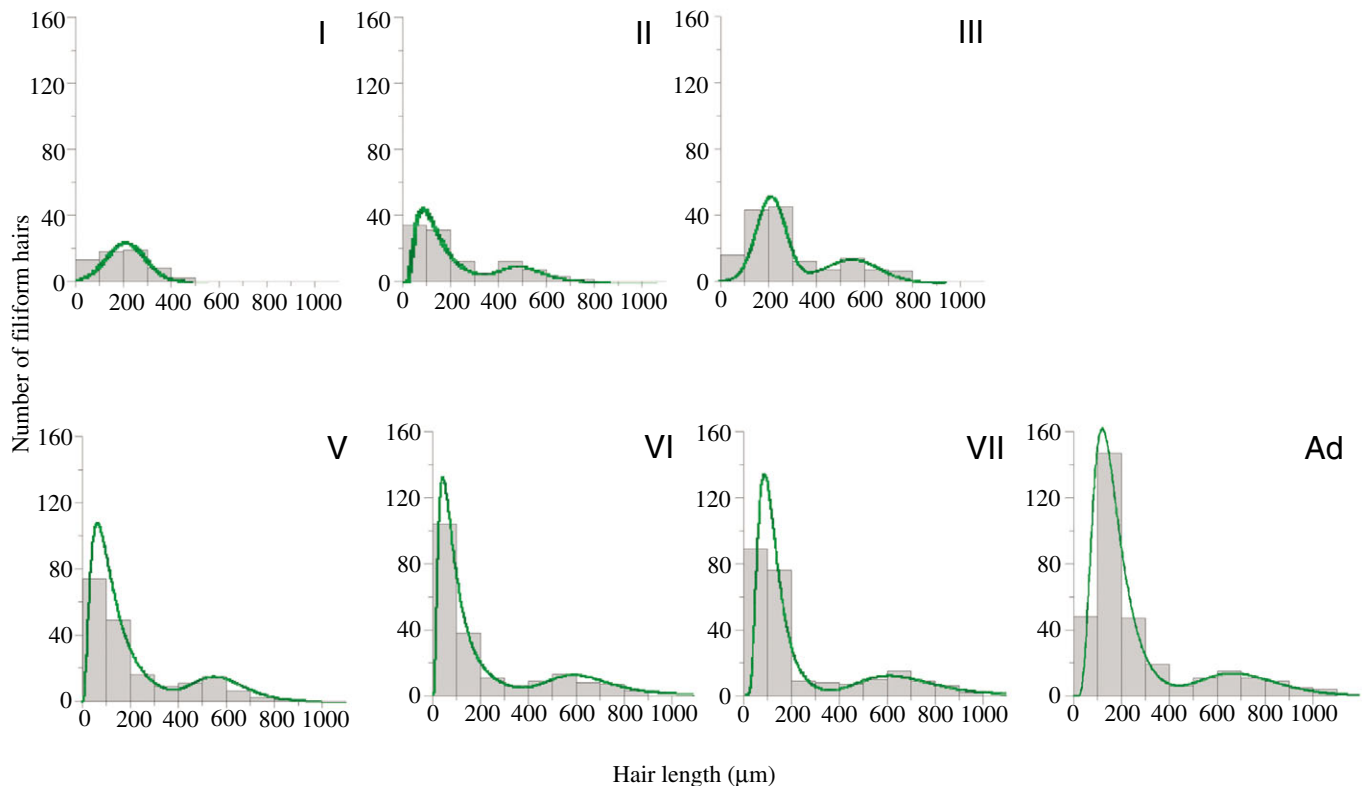


Fig. 3. Length–frequency distribution of all cercal filiform hairs inserted on the cercus throughout development in *N. sylvestris* (from instar I to adult; Ad). Adjustment curves represent the decomposition of the mixture distribution into Gaussian distributions. Parameter estimations and goodness-of-fit for each distribution are given in Table 1.

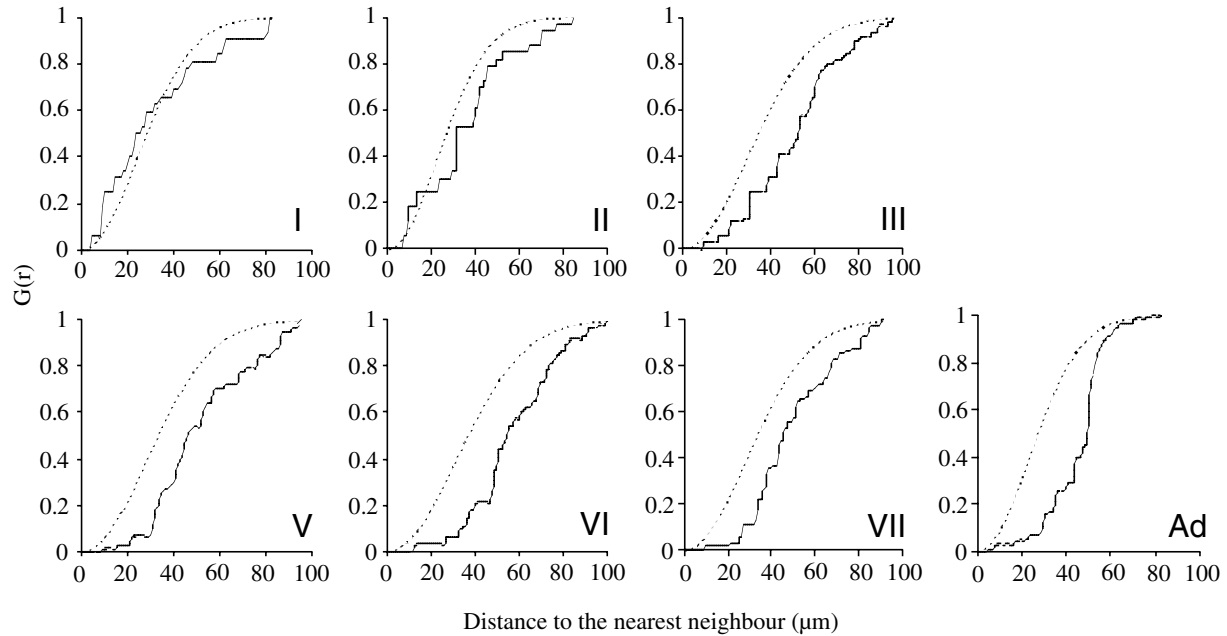


Fig. 4. Pair correlation function $G(r)$ of the cercal filiform hair point pattern throughout development (instar I to adult; Ad) in *N. sylvestris*. The broken line gives the function for the null model of complete spatial randomness.

populations of different lengths (Fig. 3). Whereas the mean of short hair populations is relatively constant throughout development ($\mu_1=142\pm 34$), the mean of long hair population progressively shifts to larger values through each instar ($\mu_2=504\ \mu\text{m}$ in instar II to $730\ \mu\text{m}$ in adult, Table 1). This increase in μ_2 is accompanied by an increase in σ_2 ($\sigma_2=90\ \mu\text{m}$ in instar II to $172\ \mu\text{m}$ in adult), as a result of an increase in maximal length of hairs as the cricket develops (from $710\ \mu\text{m}$ in instar II to $1100\ \mu\text{m}$ in adults, Fig. 3). Interestingly, the proportions of short (π_1) and long hairs (π_2) are constant during the development from instar II onwards, around 0.80 and 0.20, respectively (Table 1).

We found noticeable changes in the spatial arrangement of filiform hairs at the surface of the cercus during cricket development (Fig. 4). Whereas hairs show a random spatial pattern in early instars (I and II), they gradually move towards a regular distribution in the third, fifth, sixth and seventh instars and adults, with most hairs spaced at interval higher than $40\text{--}50\ \mu\text{m}$.

Sensitivity of the cercal array throughout development

The integration of hair length distributions into our model reveals that the cercal canopy response to an oscillating signal of various frequencies varies among cricket instars (Fig. 5A and B). The canopy response was clearly lowest in the two first cricket instars and highest in adults, whatever the air velocity or frequency. Instars III, V, VI and VII show grouped intermediate canopy responses, with ranks among instars changing across frequencies (especially instar III at $v=0.05\ \text{cm s}^{-1}$). Another emergent result from the model is the effect of air velocity on the tuning properties of the cercal canopies. Not only does the overall canopy response increase

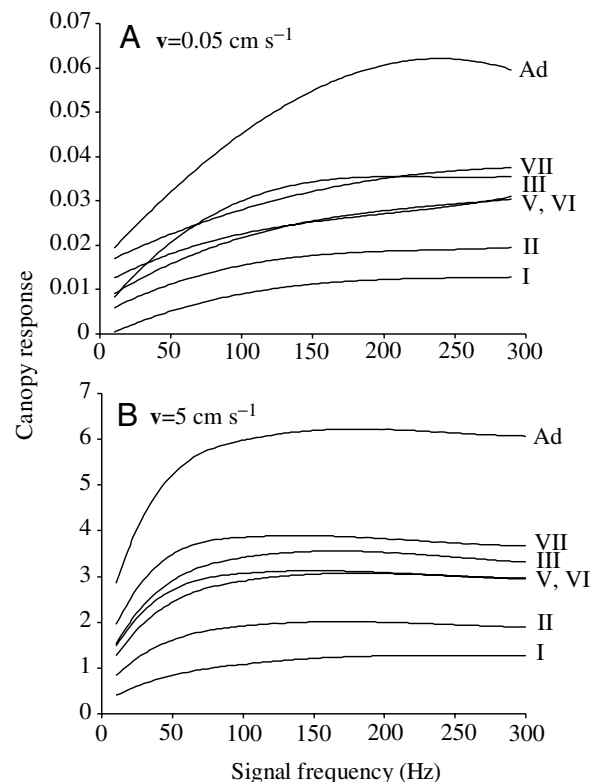


Fig. 5. Cercal hair canopy response to increasing air velocity as a function of signal frequency throughout development (instar I to adult; Ad) in *N. sylvestris*. (A) Peak air velocity $0.05\ \text{cm s}^{-1}$, (B) peak air velocity $5\ \text{cm s}^{-1}$.

at higher air velocities (Fig. 5A,B), but the perception by crickets in the lower half of the frequency range ($50\text{--}150\ \text{Hz}$)

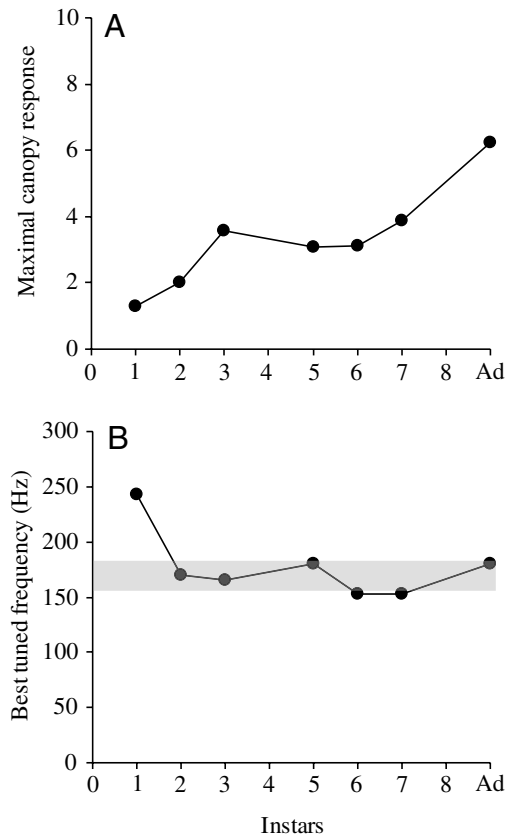


Fig. 6. Characteristics of optimal performances of the cercal sensory system throughout development (instars I to adults; Ad) in *N. sylvestris*. (A) Canopy response at best-tuned frequency; (B) value of the best tuned frequency at $v=5 \text{ cm s}^{-1}$.

is improved. This pattern is observed in all instars except the first one.

We focused on the maximum value of the response curve, which corresponds to the best sensitivity of the cercal sensory array to a given signal (Fig. 6A,B). We found that the maximal canopy response increases linearly with cricket instar ($y=0.49x+1.00$; $r^2=0.80$, Spearman rank's $P<0.001$). Contrastingly, for a given signal velocity (e.g. $v=5 \text{ mm s}^{-1}$), the best-tuned frequency is fairly constant from the second instar onwards (150–180 Hz; grey zone, Fig. 6B).

Discussion

Distinctiveness of air-sensing development in cricket

The development of the cercal hair array in crickets differs from other sensory systems in several aspects. Unlike many organisms that are born with limited sensory capabilities and do not develop important sensory structures until later in the maturation period [e.g. audition in mammals (Rubel, 1984); vision in fish (Higgs and Fuiman, 1996)], newly hatched crickets have already a developed air-sensing system. Sixty filiform hairs of varying length compose the array of each cercus of the first instar of *N. sylvestris*, a number comparable

to that observed in other cricket species [e.g. 56 in *Acheta domestica* (Kämper, 1992)]. Our model suggests that the cercal system is fully functional at this instar, capable of responding to wide array of frequencies as was experimentally shown by Kämper (Kämper, 1992) on early instars of *A. domestica*. The model also suggests that the development of optimal air-sensing acuity is fairly linear in crickets. Here again, this would contrast with other sensory systems such as visual, auditory and somatosensory systems in mammals in which there is a variation in the rate of sensory function throughout development (e.g. Berardi et al., 2000).

A surprising result of our study was the linear decrease in cercal filiform hair density throughout cricket development: whereas the increase in new filiform hairs after each moult is logarithmic, the cercal surface increases exponentially (result not shown). Two main mechanisms may explain why filiform hair increase does not follow that of cercus surface. First, other types of receptors (clavate and trichoid hairs) are inserted on the cercus as cricket grows, thus limiting the surface available to insert new filiform hairs. Second, as crickets produce longer filiform hairs after each moult, it seems that a minimal distance (40–50 μm) has to be conserved between neighbour hairs, potentially to avoid interference during oscillation (see Bathellier et al., 2005). Our spatial analyses indeed confirmed that a regular distribution of filiform hair array takes place as crickets develop.

It was also intriguing for us to find that the cercal array organisation in first instar cricket is very different from that of cockroach (*Periplaneta americana*) despite evident biomechanical, physiological and neurological similarities between the two systems (Camhi, 1984). Cockroach bears only two wind-sensitive hairs on each cercus after hatching (Camhi, 1984). Because both first-instar crickets and cockroaches have been observed to efficiently escape from predator as a result of these stimuli (Kämper, 1992) (O.D. and D.P., personal observation), the question arises as to what extent hair number affects perception and behaviour of these animals. We suppose that the benefit of having more hairs allows the detection of a wider range of signals of different types and from different directions. More generally, this dissimilarity between cricket and cockroach hair equipment underlines the fact that a specific sensory function may develop differently among related species. This has been reported, for example, within the group of electric fish in which Mormyrids are the only members to possess a complete larval electric system (Denizot et al., 1998).

Development of the bimodal length–frequency distribution of the cercal hair array

The major finding of this study is that the bimodality in hair length, underlying air-sensing function in adult crickets, is a result of changes that occur during development. Length is indeed an essential parameter of filiform hairs because the moment of inertia and the total deflecting torque applied from the air vary with length (Shimozawa and Kanou, 1984). As previously reported (Magal et al., 2006), this bimodal

distribution can explain the difference in frequency tuning of various frequencies as a function of signal intensity (Fig. 5A,B). At small air flow velocity (0.05 cm s^{-1}), crickets detect faint air movements through their long and sensitive hairs on the one hand and through a few short hairs reacting near their resonance frequencies on the other hand. As air flow velocity increases (5 cm s^{-1}) the overriding contribution of short hairs vibrating below their best frequencies produces a downward tuning shift to lower frequencies. This explains why the peak frequency of the first instar is located at higher frequency, as there are no long hairs and hence a lack of bimodality.

Another characteristic of the bimodal length–frequency distribution throughout cricket development is that, after the first moult, the proportions of short and long hairs remain constant (0.8 *versus* 0.2, respectively). As a functional consequence, the best-tuned frequency remains fairly constant throughout cricket development, between 150 and 180 Hz. This suggests that the development of the cricket cercal system is made of change and constancy: although changes in the number of hairs increase the overall sensitivity of adult crickets the value of the best tuned frequency is fixed after the second instar. Further experimental data on the evolution of hair biomechanical properties during the course of wood cricket development would be useful to refine the predictions of our model.

Ecological significance of air-sensing development in crickets

Several works have laid the hypothesis that the timing and priority of morphological changes throughout development are linked to functional demands and ecological requirements. For example, Jaeger and Hailman (Jaeger and Hailman, 1976) proposed that a shift to midspectrum (green) preference in laboratory phototactic tests of young tadpoles may be ecologically adaptive, in that it directs larvae to green plants that provide food or shelter. Similarly, ontogenetic shifts in the spectral sensitivity of cone photoreceptors observed in juvenile teleosts have been associated with changes in either habitat or diet (Shand et al., 1988; Novalés Flamarique, 2000). In crickets, one can hypothesize that changes in the sensitivity to air signals may have consequences for predator detection during life cycle. Experimental studies under both laboratory and field conditions have reported that wood crickets can be preyed upon by flying predators at various instars (Gnatzy, 1996; Dangles et al., 2006a), although little is known about their effect on population dynamics. For instance, parasitoid wasps (Sphecidae) are known to be potential predators of *N. sylvestris* (Gnatzy, 1996) and generate dominant acoustic frequencies around 150–200 Hz (Tautz and Markl, 1978; Gnatzy and Heußlein, 1986). When a cricket detects the oscillating signal emitted by a flying wasp, it stops moving, therefore trying to avoid being spotted by the wasp and to position itself for a violent kick response (Gnatzy, 1996). Other parasitoid predators such as Larinae (Hymenoptera) and Tachinidae (Diptera) also predate on crickets (Menke, 1992; Walker, 1993) and have wing beat frequencies around 200 Hz

(Wigglesworth, 1972). Wood crickets after the first moult, have been found to be best tuned to these values, suggesting that the development of the cercal array of hairs may have evolved in response to such signals. Moreover, from a physiological view point, our results support recent estimates of cercal afferent neuronal activity based on de jittered spike means, which indicate that stimulus frequency selectivity in crickets extends to ≥ 200 Hz with peak sensitivity around 150 Hz (Aldworth et al., 2005).

We also know that crickets are confronted with other types of close range, non oscillating and low frequency signals emitted by running predators such as *Liris* wasps (Gnatzy and Kämper, 1990) or wolf spiders (Dangles et al., 2006b), the latter having an outstanding impact on cricket survival in early instars (Dangles et al., 2006a). It is now therefore mandatory to observe hair movement during the attack of running predators, as the results from our simulations only strictly hold true for oscillatory signals such as those emitted by flying predators.

The authors thank two anonymous reviewers for their constructive comments on the first version of this manuscript. This work is part of the research conducted within the Cricket Inspired perCeption and Autonomous Decision Automata (CICADA) project (IST-2001-34718) and within the Customized Intelligent Life Inspired Arrays (CILIA) project (FP6-IST-016039). These projects are both funded by the European Community under the ‘Information Society Technologies-IST’ Program, Future and emergent Technologies (FET), Lifelike Perception Systems action.

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