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Directional selectivities of near-field filiform hair mechanoreceptors on the crayfish tailfan (Crustacea: Decapoda)

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Abstract Directional selectivities of mechanoreceptors that innervate filiform hairs on the crayfish tailfan were investigated with unidirectional, sinusoidal, water-motion stimuli. These recordings provide the first representative sample from filiform hair sensilla on the entire tailfan. The filiform hair receptors exhibit unimodal directional selectivity patterns that were well fitted by a cardioid function with a half-width of 122°. The preferred directions correspond to the major axis of hair motion, and are perpendicular to the orientation of lateral branches on the main hair shaft. Pooled plots of preferred directions demonstrate quadrimodal patterns on the telson and endopods which are associated with hair location, and a bimodal pattern on the exopods. For each appendage, the combination of the overall pattern of preferred directions with "coarse coding" of direction by individual receptors provides sensitivity to a full 0–360° range of water motion and the potential to discriminate the direction of water motion throughout this range. The results demonstrate several similarities to the wind-sensitive cercal receptor system in orthopteroid insects, and suggest that crustacean filiform hair receptors provide a sufficient sensory basis for behavioral orientation to water currents and shorelines.

Key words Mechanoreceptor · Filiform hair · Decapoda · Sensory coding · Behavioral orientation

Abbreviations *G6* terminal abdominal ganglion · *R2-R5* abdominal nerve roots 2–5

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Introduction

Arthropods possess a variety of cuticular hair, peg and pit sensilla which function in mechanoreception and/or chemoreception (e.g., Bullock and Horridge 1965; Bush and Laverack 1982; Derby 1982; Barth and Blickhan 1984; McIver 1985). Filiform hair receptors, the subject of this investigation, are specialized for sensing near-field movements of the surrounding fluid medium (water or air). The role of near-field receptors in giant interneuron-mediated escape response pathways is well understood in both aquatic crustaceans and terrestrial insects (reviewed by Krasne and Wine 1984; Boyan and Ball 1990). The broader functional significance of this class of mechanoreceptors, however, includes orientation to prey in crayfish and other aquatic arthropods (e.g., Murphey and Mendenhall 1973; Breithaupt et al. 1995), gravity reception in crustacean statocysts (Takahata and Hisada 1979; Neil 1993), and sensory feedback for flight stabilization in insects (Arbas 1986).

A basic functional feature of many filiform hair sensilla is their directional selectivity. Despite the extensive use of the crayfish tail as a model for mechanosensory integration, there has never been a comprehensive investigation of directional selectivity on the entire tailfan. Early physiological and morphological investigations (e.g., Mellon 1963; Kennedy 1974; Calabrese 1976; Wiese 1976) focused almost exclusively on rostrolateral regions of the telson, which are innervated by the paired fourth nerves (R4) of the terminal abdominal ganglion (G6). The results of these studies suggested that most, if not all tailfan mechanoreceptors are sensitive only to rostrocaudally-directed stimuli, a conclusion which was also initially supported by recordings from mechanosensory interneurons in G6 (Wilkens and Larimer 1972; Wiese et al. 1976; Sigvardt et al. 1982). Subsequent recordings from the mechanosensory "caudal photoreceptor" interneuron in G6 under carefully controlled stimulus conditions demonstrated maximal sensitivity to transverse (lateromedial) water movements

(Wilkens 1988; Wilkens and Douglass 1994), suggesting that a subset of mechanosensory afferents has good lateral sensitivity. This view has received additional support from anecdotal observations that long filiform hairs on the anterior medial telson are most easily displaced by transverse water movements (Schmitz et al. 1993b). The present investigation surveys, for the first time, the directional sensitivity of filiform hair sensilla on the entire tailfan.

Crayfish tailfan hair sensilla can be placed in three general categories based on their external morphology (Wiese 1976; Plummer 1984). Branched "*guard*" hairs typically occur in pairs flanking an upright receptor hair; the guard hairs lie flat on the exoskeletal surface and are putatively sensitive to tactile stimuli (Wiese 1976). The upright hairs include relatively short and stout *smooth tapered* hairs, and *filiform* hairs that are relatively thin throughout the length of the main shaft, usually "feathered" with lateral branches, and often much longer than the smooth tapered hairs (see Fig. 1 and Results).

Our results demonstrate that the directional selectivities of individual filiform hairs on the crayfish tailfan underlie a predictable pattern of overall directional sensitivity for each appendage, and show that within the horizontal plane, the tailfan displays sensitivity to all directions. These findings are important for understanding the processing of directional information by near-field mechanosensory interneurons, and the role of the tailfan in behaviors mediated by hydrodynamic signals (Schmitz 1992; Breithaupt et al. 1995). In addition, the results suggest that despite important mechanical differences between hairs in water and air (Devarakonda et al. 1996), crayfish tailfan filiform hairs share many functional similarities with the cercal filiform hairs of orthopteran insects (see Discussion).

Materials and methods

Experimental animals

The red swamp crayfish *Procambarus clarkii* was the primary species used in this study. A few experiments were performed on the White River crayfish, *P. acutus*, and the papershell crayfish, *Orconectes immunis*; the latter collected locally in the Meramec River, Missouri. *P. clarkii* and *P. acutus* are sympatric in the Mississippi flood plains of southeast Missouri and regions further south. Consistent data were obtained from each species (see Results for details). Although both *P. clarkii* and *P. acutus* were obtained initially from the Atchafalaya Biological Supply (Raceland, La.), nearly all experiments were conducted on *P. clarkii* reared in tanks located in a greenhouse. Crayfish were fed chopped carrots and pelleted trout chow (Purina), and provided with small clay pots for hiding places. Laboratory-reared crayfish were used to insure that experimental animals had undamaged filiform hairs, as those shipped commercially are often damaged or infested with ectocommensal branchiobdellid annelids. Small to medium-sized intermolt male and female crayfish, 3–10 cm total length rostrum to telson, were used in experiments; most animals were 6–7.5 cm long.

Dissection and physiological recordings

Mechanoreceptor activity was recorded from filiform hairs on isolated tailfan appendages. Crayfish were decapitated, and the abdomen was severed and immersed in crayfish saline (modified from van Harreveld 1936; buffered with 4.2 $mmol \cdot l^{-1}$ HEPES, pH 7.2). A single appendage was isolated with its corresponding sensory nerve root(s): exopod and root 2 (R2), endopod and root 3(R3), or telson and paired roots 4 and 5 (R4 and R5; Calabrese 1976). For stimulation and recording, nerve roots of larger individuals were immersed for approximately 1 min in saline containing 1% protease (Protease E, Sigma), partially digesting the nerve sheath to provide larger-amplitude action potentials. Appendages were then fixed to the shaft of an electromechanical transducer (Pasco Mechanical Wave Driver, SF 9324), and the preparation was placed on a vibration isolation table TMC, 78 Series).

The stimulus paradigm employed for physiological recordings is of a new design, the details and advantages of which are fully described elsewhere (Wilkens and Douglass 1994). Briefly, the appendage was pinned vertically to a platform composed of a small Lucite frame filled with silicone elastomer (Dow Corning, Sylgard). The platform and transducer shaft oscillated vertically in a stationary saline-filled bath ($L \times W \times H = 7.5$ cm $\times$ 5 cm $\times$ 5 cm) with transparent glass sides, such that upward movements of the appendage were equivalent to downward water motions. A horizontal axle permitted rotation of the platform in the plane of the appendage through an effective range of 360°, such that the vertical movements simulated stimulus currents directed from antero-posterior through medio-lateral angles (see Fig. 2 in Wilkens and Douglass 1994). Vertical movement of the appendage in a stationary aquatic medium reduces or eliminates stimulus artifacts arising from traveling waves that would otherwise compromise stimulus-response measurements in near-field receptors. The stimulus movements were unidirectional and sinusoidal, corresponding to a 1.5-Hz cosine wave with a 0.5-s delay inserted at $t = \pi$ radians relative to the onset of stimulation (see Fig. 2). This waveform avoided sudden on-off transients, and the delay at mid-cycle permitted a clear separation of the responses to opposing unidirectional stimuli. The modified cosine wave was generated with a function generator (Tektronix, FG501) controlled by external trigger and gate pulse inputs (Wilkens and Douglass 1994). The output was fed to a power amplifier, and signal amplitude was controlled in 10- and 1-dB steps with VHF series attenuators (Hewlett-Packard, 355C and 355D).

Stimulus amplitude was calibrated and standardized prior to each experiment by viewing the transducer shaft movements from the side with a dissecting microscope. This method provided accurate measurements of displacement amplitudes as small as 30 μm. Alternatively, a laser beam was focused on a small mirror held between the transducer shaft and a stationary post, and a photodiode array recorded changes in the position of the reflected beam. This method resolved the transducer movements to ca. 0.1 μm peak-to-peak.

Afferent spiking activity was recorded from the nerve roots using standard extracellular recording methods. A small (30–65 μm inner diameter) saline-filled suction pipette attached to the mounting platform was connected to the amplifier inputs by a thin polyethylene tube and fine silver wire leads that did not interfere with stimulus movements or rotation of the preparation. Impulses were AC preamplified (WPI, DAM6), monitored with an oscilloscope and loudspeaker, and single units were isolated with a dual-threshold window discriminator (WPI, 121). Units that were sensitive to low-frequency water movements were selected for further study. To locate the hair associated with the windowed spikes, an electrolytically sharpened tungsten needle mounted on a micromanipulator was used to gently deflect hairs one by one while viewing the probe tip with a microscope. Deflection in a "preferred" direction increased the spike rate, and deflection in the opposite direction sharply decreased the background activity, confirming that the windowed spikes originated from only that hair. For receptors exhibiting very low background spiking, similar confirmation was obtained by demonstrating a reduction in exci-

tation when the hair tip was held in a non-preferred position while continuing the stimulus movements of the appendage.

Receptor responses were analyzed with peri-stimulus time histograms, displayed on-line and stored to computer disks for subsequent analysis. Initial experiments were performed using a Nicolet MED-80 computer (Madison Wis.); later experiments employed a Brainwave 80486 PC with Experimenter's Workbench data acquisition and analysis software (Datawave Technologies, Longmont, Colo.). After a single unit (occasionally two; see Results) was windowed and its hair identified, responses to different stimulus amplitudes were tested with the appendage at an arbitrary angle to establish a moderately suprathreshold stimulus amplitude. The amplitude was then held constant while testing responses to changes in stimulus direction at 30° intervals, followed by tests at the intervening angles, producing an overall record spanning 360° at 15° intervals. At the conclusion of the recording session the hair was again probed to confirm its identification with the windowed spikes.

Hair movement, morphology, and uropod postures

At the start of most recordings, a sketch of the appendage in the vicinity of the hair was made under low-power microscopy so that subsequently the hair could be reidentified for hair mobility and/or dimension measurements. Hair movements relative to stimulus direction were measured using a second stimulation chamber employing an alternative method of vertical stimulation (see Fig. 1, Wilkens and Douglass 1994). Here, the appendage was held stationary while the fluid oscillated sinusoidally at 1–10 Hz. The hairs were observed in dorsal view at $\times$ 80 and illuminated with a strobe (General Radio, Strobotac 1531-AB) that was triggered by the function generator following an adjustable delay (Grass Instr., S48 stimulator). By varying the delay, the maximal hair displacements could be visualized and measured at various stimulus directions using an ocular micrometer.

For hair length measurements, a small section of the cuticle (approximately 2 mm $\times$ 2 mm) containing the identified hair was excised and mounted on a rotating shaft in a small saline-filled chamber. This procedure permitted the hair to be oriented within the focal plane, sketched with a camera lucida, and its dimensions measured at $\times$100.

The typical range of uropod postures during forward walking and alert standing was recorded on videotape. The orientation of the exopods and endopods was defined as the angle between the longitudinal axis of the telson and the proximo-distal ridge on the dorsal surface of each appendage.

Data analysis

Peri-stimulus time histograms were calculated on-line by counting the single-unit spikes in 15-ms bins and summing the histograms from 15 presentations of the modified cosine stimulus repeated at 2-s intervals. Responses to unidirectional stimuli were defined as the numbers of spikes that occurred between stimulus onset and maximum stimulus velocity in either the upward ($t = 0$ to $\pi/2$) or downward ($t = \pi$ to $3\pi/2$) direction (see Results, Fig. 2), and were used to construct polar plots of directional selectivity (Results, Fig. 3). Spike counts were limited to the accelerating phase of the stimulus in order to exclude spikes during return motion of the hair toward its resting position (against the stimulus direction). This return motion is due to the spring-like articulation of the hair with the exoskeleton, and can begin before the end of each unidirectional phase of the water motion (see Results).

Each response defines a vector (r, θ), where r is the number of spikes counted and θ is the direction of water movement relative to the appendage. The same vector can be defined in Cartesian coordinates (x, y), where $x = r \cdot \cos(\theta)$ and $y = r \cdot \sin(\theta)$. The *mean response vector* is obtained from the averages of the x and y components of individual responses:

$$\overline{X} = \sum r_i \cdot \cos(\theta_i);\ \overline{Y} = \sum r_i \cdot \sin(\theta_i)\ , \qquad (1)$$

and, assuming a unimodal directional selectivity pattern, the *preferred direction* is the angle defined by the mean response vector (Batschelet 1981). The larger the magnitude of the mean response vector, the more directionally selective are the responses.

Patterns of directional selectivity were compared by plotting the preferred directions of receptors belonging to a particular appendage or sensory nerve root. The Rayleigh Test (Batschelet 1981) was used to test the hypothesis that the preferred directions were drawn from a uniform circular distribution. As will be seen in the Results, each pattern of preferred directions suggested either a bimodal or quadrimodal distribution. The raw preferred directions therefore were transformed to yield unimodal distributions, as required for application of the Rayleigh Test (see Batschelet 1981).

Results

We investigated the directional selectivities of individual filiform sensilla on the crayfish tailfan with respect to hair morphology, hair mobility, and responses of the receptors to unidirectional, sinusoidal, water motion. The overall organization of directional selectivity was then analyzed on each appendage and on the tailfan as a whole.

Morphology and fluid-coupled movements

Filiform sensilla are restricted mainly to the dorsal surfaces of the tailfan including the telson and lateral (non-overlapping) half of each uropod. The filiform hairs (Fig. 1A) are characterized by a thin, gradually-tapering shaft, 7–15 μm wide at the base, and range in length from less than 100 μm to at least 1000 μm. Variable numbers of lateral branches extend outward and distally for up to 80 μm, giving the hairs a feather-like appearance. An important feature of the lateral branches is their tendency to be constrained toward a single plane. In shorter hairs, branching is typically profuse and occurs along all but the most proximal portions of the shaft, whereas branching is sparse or absent in longer hairs, and occurs primarily along the distal half of the hair shaft. Figure 1B compares a census of tailfan filiform hair lengths measured from three *P. clarkii* (light bars, $n = 184$) with the length distribution observed in filiform hairs from which recordings were made (filled bars, $n = 76$). In both distributions, approximately 80% of all filiform hairs fell within the range 50–500 μm, with a few longer hairs ranging from 500 μm to nearly 1000 μm. Although the very shortest filiform hairs evidently were missed during recordings, the physiological sample is otherwise representative of a typical length distribution. Smooth tapered hairs (Fig. 1A, rightmost hair) were much shorter, stouter and less variable in length than the filiform hairs. Occasional measurements of smooth tapered hair lengths on *P. clarkii* tailfans including one complete survey ($n = 32$), showed a range of diameter from 19 μm to 22 μm at the base, and

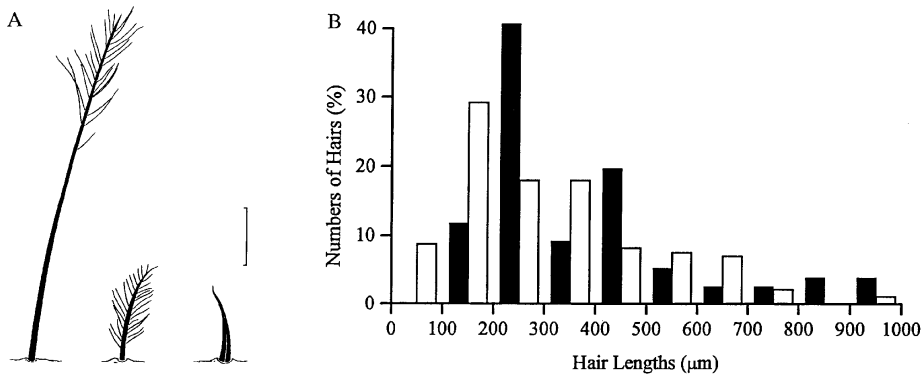


Fig. 1A, B Filiform hair morphology and length distributions on the crayfish tailfan. **A** Schematic illustrations of typical long (*left*) and short (*middle*) filiform hairs with a smooth tapered hair (*at right*) included for comparison, (guard hairs not shown). *Scale bar* 100 μm. **B** Histogram comparing the distribution of filiform hair lengths (0–99, 100–299 μm, etc.) censused from three *P. clarkii* (*open bars*, two complete tailfans and the right half of a third, mean percentages weighted for the individual sample sizes of 65, 61 and 58), with the distribution of *P. clarkii* filiform hairs identified during single-unit recordings (*filled bars*, $n = 76$)

lengths from 70 μm to 270 μm, with 75% between 100 μm and 200 μm.

Filiform hair deflections in response to water movements are orientation selective, and the preferred orientation can be predicted to a first approximation by observing the orientations of the lateral branches. In on-axis views of the hair, the profiles of the branches were generally confined within an elliptical region approximately perpendicular to the preferred direction of hair movement. The paired guard hairs, in contrast, were invariably aligned parallel to the proximal-distal axis to each appendage, and therefore were not accurate indicators of directional sensitivity. A representative example of filiform hair movements in response to a sinusoidal, fluid-coupled stimulus is illustrated in Fig. 3A. Although there was some mobility in all directions, the overall pattern was bimodal, in this case with the largest deflections during transverse motion relative to the longitudinal axis of the appendage.

Physiological responses

Sensory receptors innervating the filiform hairs, including different receptors recorded from a single preparation, exhibited various levels of spontaneous or background activity. In unstimulated preparations, some cells produced only occasional action potentials while others averaged spike rates of 3–5 Hz. In contrast with the variability among receptors, the activity of individual receptors was remarkably stable. For example, the cell whose activity is illustrated in Figure 4A maintained a statistically uniform discharge rate (ca. 1.5 Hz) for at least 2.5 min (*G*-test for goodness of fit, $P > 0.5$). Responses to periodic near-field water movements were also stable, showing little or no adaptation for periods of up to several minutes (Fig. 4B).

Figure 2 illustrates the characteristic directional responses of filiform hair mechanoreceptors to fluid-coupled sinusoidal stimulation. In this example, the initial displacement was in the direction of maximal sensitivity. The excitatory response was characterized by a rapid increase in spiking activity immediately following stimulus onset. Peak discharge rates for low-frequency stimuli coincided with the portion of the stimulus cycle (interval $a, t = 0$ to $\pi/2$) where stimulus velocity accelerated to a maximum. Qualitative observations suggest that hair displacement in the preferred direction also reached a maximum during this phase of the stimulus. As stimulus velocity diminished ($t = \pi/2$ to π), the spiking activity decreased rapidly. The onset of stimulation in the opposite direction (interval $b, t = \pi$ to $3\pi/2$) reduced the background activity as the hair was displaced in the non-preferred direction for this receptor. A

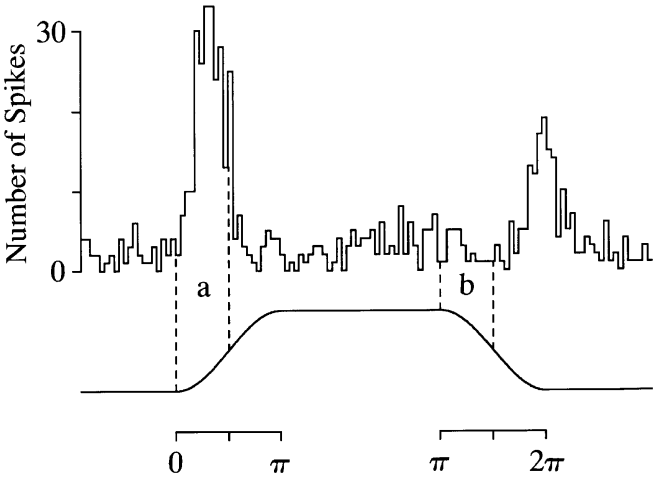
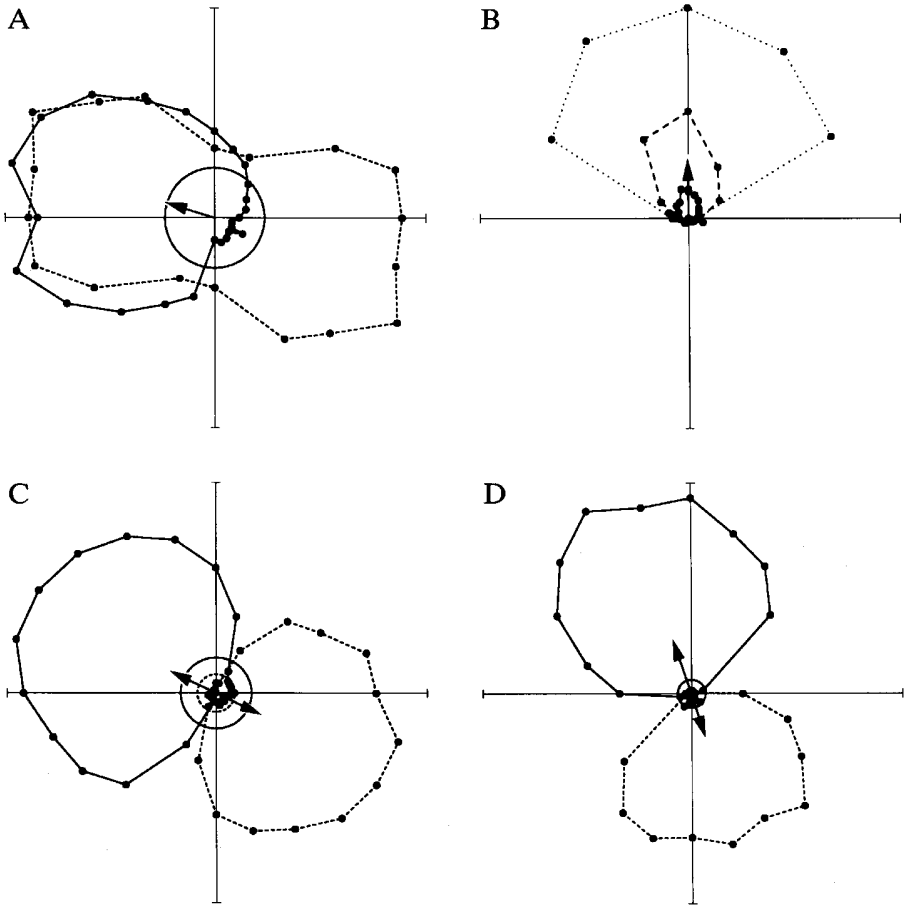


Fig. 2 Cumulative peri-stimulus time histogram (*upper trace*, bin width = 15 ms) of single-unit spiking in a representative filiform hair receptor during 15 cycles of stimulation with 1.5-Hz, unidirectional sinusoidal water movements. The *lower trace* schematically illustrates the time-course of water displacement during a single stimulus cycle in which two 1.5-Hz, unidirectional sinusoidal water movements were separated by a 500-ms delay. Data from similar histograms were used to obtain directional selectivity plots (e.g., Figs. 3, 5) from the numbers of spikes during the initial stimulus movements (*intervals a and b*, duration $= \pi/2$) at each of 12 appendage orientations to the transducer shaft (see Methods), yielding 24 stimulus directions spanning 360°

secondary discharge peak began during the final stimulus phase ($t = 3\pi/2$ to 2π), where stimulus velocity in the non-preferred direction decelerated. The second excitation was due to the return motion of the hair in the excitatory direction as the diminishing water velocity became insufficient to maintain hair deflection in the non-preferred direction. This conclusion is based upon visual observations of hair motions during recordings, while deflecting the hair with either the tungsten probe or the sinusoidal water motion stimulus. Increased spiking occurred during any hair movement in the preferred direction, whether the hair was moving away from its resting position, or returning from a previous deflection in the non-preferred direction. Similar phase relationships between the stimulus motion and spike timing were observed in all recordings from filiform hairs. Mechanosensory interneurons in the terminal ganglion also show similar response dynamics during low-frequency, unidirectional, fluid-coupled stimulation (see Fig. 2 in Wilkens 1988).

Polar plots of directional selectivity were constructed by summing the numbers of action potentials in intervals *a* and *b* of response histograms obtained at various stimulus orientations. In contrast with the bimodal movement profiles of hairs (Fig. 3A), individual receptors exhibited strictly unimodal directional selectivity patterns (Fig. 3A–D). As illustrated in Fig. 3A, the directional selectivity of receptors corresponded closely with the motion of the hair during fluid-coupled stimulation. Similar results were obtained in several additional physiological recordings from relatively long filiform sensilla followed by measurements of the hair motions. Although shorter filiform sensilla exhibited very small

Fig. 3A–D Directional selectivities of single filiform hairs and hair receptors. Proximal is upward and defined as 0°, *arrows* show preferred directions and mean response vector amplitudes, and *circles* centered at the origin in **A**, **C**, **D** illustrate the mean background spiking activity of the corresponding receptors, measured at two or more appendage orientations. Background activity in **B** was negligible. **A** comparison of the directional selectivity of a left endopod filiform receptor (*solid trace*, numbers of spikes versus direction of water motion) with the directional mobility of the corresponding hair (*dashed trace*, hair tip displacements during constant-amplitude water motion; hair length = 880 μm). The preferred direction of this receptor was 73.3°. **B** Directional selectivity of a single unit on the left endopod, tested at three stimulus amplitudes of 4.5 μm (*solid trace*), 25 μm (*dashed*), and 250 μm (*dotted*), and showing very little difference among the corresponding preferred directions (5.0°, 2.0° and 0.8°, respectively; *arrow* shows the mean of these three preferred directions). Hair length = 472 μm. **C**, **D** Examples of simultaneous recordings from dually innervated hairs, illustrating the characteristic precision with which the preferred directions of the two receptors are opposed. **C** Left exopod (R2), preferred directions = 64.9° (*solid trace*) and 244° (*dashed*); hair length = 352 μm. **D** Telson (left R4), preferred directions = 19.5° (*solid trace*) and 197.4° (*dashed*); hair length = 308 μm. Numbers of spikes and hair displacement units were normalized to a unit radius (*axis tics*). Stimulus amplitudes for **A**, **C** and **D** were 45 μm



motion amplitudes that could not be precisely measured, the observed directions of greatest mobility were also consistent with the preferred directions of the associated receptors. As illustrated in Fig. 3B, preferred directions were affected little by stimulus amplitude ($n = 4$ hairs), although larger displacements tended to broaden the angular response function.

In 21 experiments it was possible to discern by their spike amplitudes the activity of two receptors that innervated the same filiform hair. Although action potentials from one of the two units were often difficult to distinguish from background activity due to their small amplitude, manipulation of the identified hair invariably revealed that the most effective excitatory stimuli for each of the two units were in opposite directions. Simultaneous recordings and analyses of directional responses were obtained from five such pairs of receptors that provided clearly windowed spikes. The data from two of these receptor pairs are illustrated in Figs. 3C and 3D. In all five pairs, the difference in preferred directions was consistently near 180° ($\overline{X} = 178.8° \pm 3.4°$ SE). No more than two receptor cells were ever detected in association with a single filiform hair.

The relationship between water movement direction (θ) and receptor response (R) was examined by setting the preferred direction of each receptor equal to zero, normalizing the minimum and maximum number of spikes to 0 and 1, respectively, and pooling the data on a single plot (Fig. 5). These data are well described by a cardioid of the form

$$R(\theta) = (1 + \cos\theta)^a / 2^a \quad , \qquad (2)$$

where $a = 2.295$ gives the best fit (Fig. 5, thick line). The value of a determines how broad or narrow the function is. Thus, under the stimulus conditions employed, the preferred directional selectivity function of these receptors was considerably narrower than a standard cosine function ($a = 1$, thin line in Fig. 5), with a half-width of approximately 122° instead of 180°.

Patterns of directional sensitivity on individual appendages

Each appendage showed a distinctive overall pattern of filiform hair receptor directional sensitivity. These patterns are illustrated in Fig. 6, which shows preferred directions relative to the longitudinal (proximal-distal) axis of each appendage (Fig. 6A–E) or the anterior-posterior axis of the animal (Fig. 6E, F). On the exopods, preferred directions on both the left and right appendages (Fig. 6A and B, respectively) were clustered in symmetrical bimodal distributions (A, $P < 0.03$, $n = 15$; B, $P < 0.01$, $n = 9$) oriented obliquely to the appendage longitudinal axis. Significantly, all but one exopod receptor exhibited preferred directions within two opposing quadrants, regions that represent only 50% of the available angular range. In contrast, the

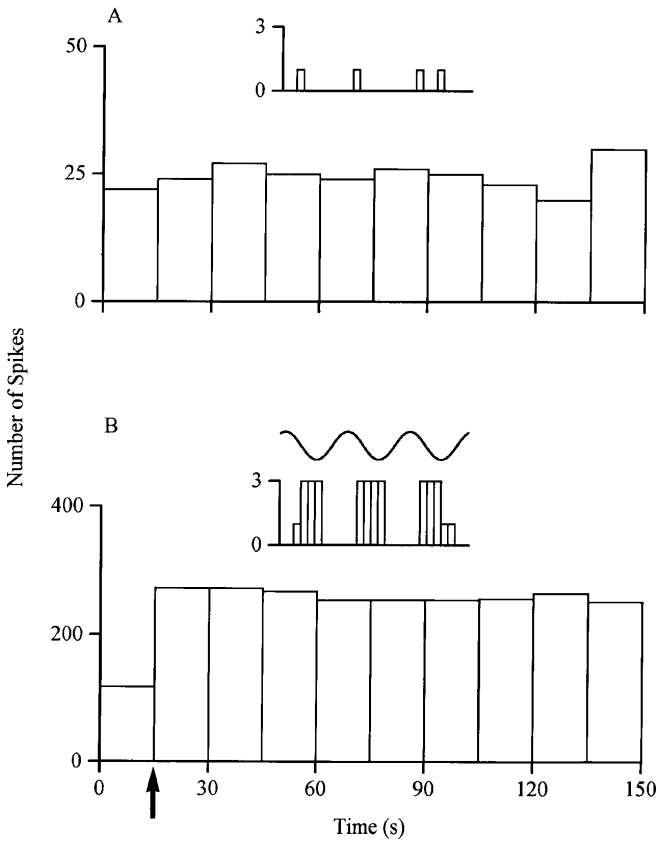


Fig. 4A, B Tonic spiking of filiform hair receptors with and without stimulation. **A** Low-frequency background spiking in a telson receptor recorded from the right fourth nerve root (hair length = 267 μm). **B** Spiking in a right exopod receptor (root 2) shown before and after onset (*arrow*) of stimulation with sinusoidal movement (45 μm peak-to-peak amplitude, hair length = 440 μm). **A** and **B** *insets* illustrate spiking activity at a finer temporal resolution (bin width = 75 ms), and the relationship of spike times to the phase of the stimulus cycle (*sinusoidal trace* above **B** inset)

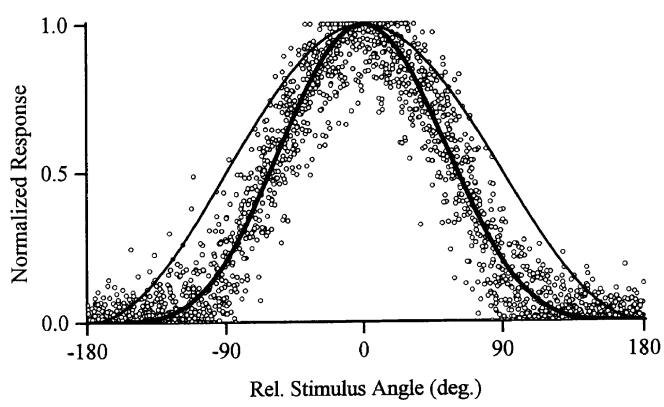


Fig. 5 Responses of 95 filiform receptors to unidirectional water motion, with stimulus angles zeroed to the individual preferred directions (see Eq. 1) and responses (*open circles*) normalized to the minimum and maximum numbers of action potentials for each receptor. *Thick trace*, best fit to the cardioid function of Eq. 2, with $a = 2.295$ (curve-fitting with Microcal Origin 3.5, Northampton, Mass.). A standard cosine (*thin trace*, $a = 1$) is shown for comparison

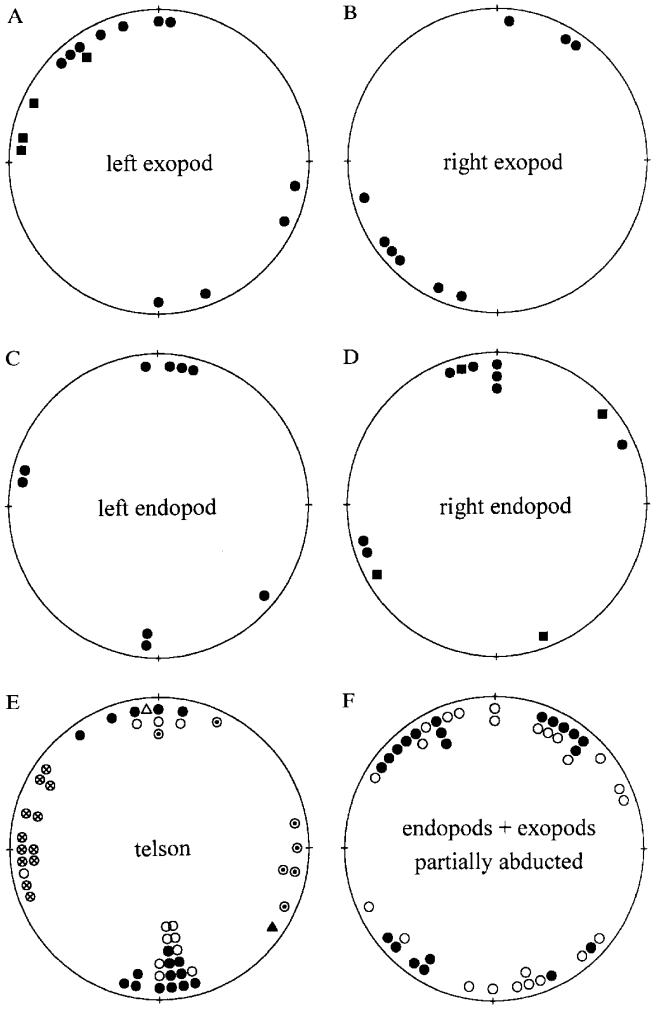


Fig. 6A–F Patterns of directional sensitivity of 95 filiform hair receptors, illustrated for individual tailfan appendages **A–E** and pooled from the four uropod appendages **F**. The left **A** and right **B** exopods both show bimodal patterns, whereas left **C** and right **D** endopods and the telson **E** show quadrimodal patterns (see Results for test statistics). Each point represents the preferred direction, computed from a single-unit recording using Eq. 1 and rounded to the nearest 5° interval. Angels are plotted relative to the longitudinal axis of either the appendage (**A–E**, with proximal upward) or of the crayfish (**F**, with rostral upward). In **F** the endopods are held at +/− 25° and the exopods at +/− 65° from the caudal direction. Symbol shapes in **A–E** denote the species (*circles*, *Procambarus clarkii*; *squares*, *P. acutus*; *triangles*, *Orconectes immunis*. In **E** and **F**, symbol fill patterns denote either **E** the nerve root from which each recording was obtained (*filled*, left R4; *open*, right R4; *dotted*, left R5; *cross hatched*, right R5), or **F** the type of uropod appendage (*filled*, endopods; *open*, exopods)

endopod receptors (Fig. 6C, D) exhibited quadrimodal patterns of directional sensitivity (C, $P < 0.001$, $n = 9$; D, $P < 0.005$, $n = 12$) with preferred directions clustered about longitudinal and oblique axes. The eight recordings from *P. acutus* exopods and endopods (filled squares) were consistent with the patterns observed in *P. clarkii*, and were included in the Rayleigh tests.

The telson also showed a strongly quadrimodal overall pattern of preferred directions, which can be decomposed into two bimodal patterns that are related to the nerve root associated with each receptor and to hair location on the telson. Recordings from left and right R4 nerve roots (Fig. 6E, filled and open symbols, respectively) produced a bimodal pattern oriented along the rostrocaudal axis ($P \ll 0.001$, $n = 31$), with maximal sensitivities almost invariably restricted to a narrow range of anteriorly or caudally directed water movements. The two exceptions to this trend were also atypical in other respects. The only leftward-sensitive cell (Fig. 6E, open circle at left) was associated with a hair on the medial anterior telson (see Fig. 7), a location bordering the receptive field for R5 (Calabrese 1976). The second exception (caudolateral sensitivity, filled triangle) represents one of two recordings from *Orconectes immunis*. Recordings from left and right R5 (Fig. 6E, dotted and cross-hatched circles, respectively) also showed a bimodal pattern ($P < 0.001$, $n = 19$), but unlike R4 receptors, R5 receptors were almost exclusively sensitive to lateral or oblique water movements. Here, the two exceptions were rostrally sensitive cells that both were located on the caudal and caudolateral telson (see Fig. 7). In summary, telson filiform hair receptors were sensitive mainly in lateral or rostrocaudal directions. Although these two preferred orientations were clearly associated with recordings from R5 and R4, respectively, preferred directions were also related to the locations of the hairs on the telson (see below).

Patterns of directional sensitivity on the tailfan

Uropod angles with respect to the rostrocaudal axis of the crayfish were measured from videotapes of unrestrained *P. clarkii* ($n = 4$ animals) while walking or standing in a typical alert posture in which the tailfan is held approximately parallel with the substrate. The posture of the endopods varied little, their longitudinal axes ranging from ca. 20° (adducted) to 30° (abducted) from the posterior direction, whereas exopod postures exhibited a broader range from ca. 30° (adducted) to 70–80° (abducted). Figure 6F illustrates the pattern of preferred directions pooled from the four uropods, assuming partially abducted postures of 25° for the endopods and 65° for the exopods. The overall pattern is bimodal ($n = 45$, $P < 0.006$), with preferred directions clustered rostrally and caudally, and the bimodality is due mainly to the exopods. Full adduction (not shown) further increases the bimodal bias, while full abduction produces a more uniform pattern.

In addition to the appendage-specific distributions described above, each appendage exhibited a distinct spatial pattern of preferred directions. Figure 7 combines the preferred direction data from 95 receptors with the known locations of the associated filiform hair sensilla on the tailfan. As in Fig. 6F, the uropods are shown at intermediate positions between the fully adducted and abducted postures. On both the endopods and telson, separate longitudinal columns of hair receptors can be

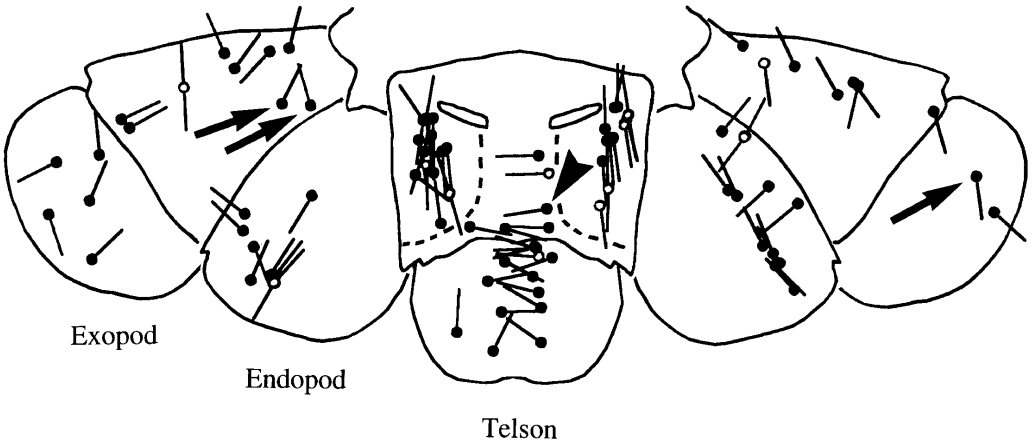


Fig. 7 Overall pattern of directional selectivity of 95 filiform hair receptors on the crayfish tailfan. As in Fig. 6F, the uropods are held at $+/-65°$ (exopods) and $+/-25°$ (endopods) from the caudal direction; these positions are intermediate between the minimum and maximum angles measured from unrestrained *P. clarkii*. *Dashed lines* on the telson (after Calabrese 1976) indicate borders between the receptive fields of paired sensory nerve roots 4 (anterolateral telson) and 5 (medial and posterior telson). *Dots* indicate hair locations, and the attached *unit vectors* show the preferred directions. *Open circles*, 12 hairs known to have been dually innervated and which yielded quantifiable directional response data from at least one of the two receptors. *Arrows* indicate three ventral hairs, recorded from the left expod of *P. acutus* and the right exopod of *P. clarkii*. The *arrowhead* on the telson marks an unusual R4 sensillum that was located within the typical R5 receptive field and was most sensitive to medial motion

distinguished, the preferred directions of which were almost exclusively longitudinal or transverse: on the telson, the more medial sensilla responded best to transverse motion, including most R5 sensilla and the aforementioned R4 sensilla (Fig. 7, filled arrowhead) located within the typical receptive field for R5. Among both the laterally and the most-posteriorly positioned telson filiform hairs, however, all but one were at least partially sensitive to longitudinal (rostrocaudal) motion, regardless of whether their axons projected to nerve root R4 or R5. In a reversal of the telson pattern, medial endopod receptors were sensitive longitudinally, and lateral receptors, transversely. Meanwhile, the exopods showed no clear relationship between receptor locations and preferred directions, although the directional properties of the three recorded ventral filiform hair sensilla (Fig. 7, arrows) were consistent with the overall pattern observed on the dorsal surfaces. Together, these data indicate that the development of the preferred directions of filiform hair sensilla depends more upon receptor location on the surface of the tailfan than on the identity of the sensory root to which the receptor axon projects.

A striking feature of the R5 recordings was that all but one of the preferred directions measured from R5 receptors pointed medially (Fig. 7), as if the corresponding hairs had unusually restricted mobility or were only singly innervated. Other observations, however, refute both conclusions: filiform hairs within the R5 receptive field are as easily deflected by leftward as rightward water motion, and there is considerable evidence for dual innervation of crayfish filiform hairs (see Discussion), including two of the R5 recordings (Fig. 7). All R5 filiform hairs seem likely to be dually innervated, but perhaps some shared biophysical feature of the medially sensitive receptors makes them more accessible to recordings.

Discussion

General conclusions

The directional sensitivity of the crayfish tailfan to low-frequency, low-velocity hydrodynamic stimuli was investigated by recording from the receptors of identified filiform hair sensilla during stimulation with unidirectional water motion. All filiform hair receptors exhibited unimodal directional selectivity patterns. This type of pattern is consistent with virtually all previous recordings from filiform hairs, including raw spike traces from crayfish (Wiese 1976) and directional selectivity plots from insect filiform hairs (Tobias and Murphey 1979; Westin 1979). The only exceptions to this trend are two bimodal patterns recorded from telson receptors stimulated with motion of a wire loop and involving relatively large-amplitude displacements (Wiese 1976).

Whereas previous studies at the receptor level have focused on properties of telson receptors innervated by nerve R4, and have suggested almost exclusively rostrocaudal sensitivity, primary mechanosensory interneurons in G6 that receive tailfan inputs include units with maximal sensitivity to leftward or rightward motion (see Introduction). Until now, the sensory basis for these transverse sensitivity maxima has been uncertain, as a system limited mainly to rostrocaudally sensitive hairs would discriminate poorly between leftward and rightward motion. Our results clearly establish that the directional tuning characteristics of filiform hair receptors on each tailfan appendage provide a basis for unambiguous directional discriminations (see below). Although contralateral inhibition may refine the ipsilateral directional information (cf. Marzelli and Wilkens 1979), there is no need to invoke central integrative

mechanisms (Miyata et al. 1997) to explain the directional properties of primary interneurons in G6.

The present recordings from *P. clarkii* mechanoreceptors ($n = 85$) constitute a representative sample of tailfan filiform sensilla, as the length distribution of their associated hairs ($n = 76$) mirrors the mean length distribution in complete censuses of *P. clarkii* tailfans ($n = 2.5$). The recordings encompassed sensilla from virtually all tailfan regions containing filiform hairs, including one ventral hair. The similar preferred direction measurements from a small sample of *P. acutus* and *Orconectes immunis* hairs ($n = 10$) suggest that among epigeal freshwater crayfishes, interspecific differences in receptor physiology or in the spatial arrangement of directional classes are minor. In contrast, scanning electron micrographs of tailfans of a blind cave crayfish (*P. orcinus*) suggest that in this cavernicolous species, there is a dramatic shift toward longer filiform sensilla (L. A. Wilkens, unpublished observations).

The numbers of mechanoreceptor neurons reported to innervate individual crustacean mechanosensilla vary from two in filiform hairs (Mellon 1963; Kennedy 1974; Wiese 1976) to two to three in crustacean statocysts (Bush and Laverack 1982). Consistent with the earlier observations of filiforms hairs, our recordings revealed up to two mechanoreceptors. The present investigation, however, focused specifically on tonic receptors that respond to gentle water motions, thus omitting receptors with more phasic properties. Moreover, ultrastructural observations on crayfish filiform hairs (Wiese 1976) suggest that some hairs may be innervated with three or more receptor neurons. Since crustacean mechanoreceptive sensilla are often accompanied by chemoreceptors (Derby 1982; Hatt 1986; Mesce 1993), any additional receptor(s) could be either phasic mechanoreceptors or chemoreceptors.

Directional tuning and coding in filiform hair receptors

The broad, unimodal patterns of directional selectivity exhibited by crayfish filiform hair mechanoreceptors result from a combination of mechanisms. First, structural features of the hairs and their articulation with the exoskeleton constrain them toward a single preferred plane of movement. Although ultrastructural observations of the articulation in crayfish suggest a loose hinge-like arrangement (Wiese 1976), morphological anisotropies in the articulation do not necessarily correspond to directionality of spider trichobothrial filiform hairs (Barth et al. 1993). An alternative possibility, supported by experimental evidence from cricket cercal hairs (Kanou et al. 1989), is that the directionality arises from a spring-like mechanism at the base of the hair. The present investigation suggests a third structural mechanism in filiform hairs that have lateral branches: the roughly coplanar distribution of the branches will preferentially increase hydrodynamic drag (cf. Vogel 1994) and amplify displacements of the hair shaft in a direction orthogonal to the branches. Any of these purely morphological mechanisms may explain the observed *bimodal* patterns of hair mobility, but not the unimodal directional selectivity of receptor neurons. Unimodality presumably arises from asymmetries in the dendrite terminals at the base of the hair (Bush and Laverack 1982; French 1988). There may, for example, be asymmetries in the attachment of the dendrite to the base (Mellon 1963), or in the spatial distribution of stretch-sensitive channels within the dendritic membrane.

Broadly tuned responses to motion direction are characteristic of various arthropod mechanoreceptors (cf. Reissland and Görner 1978; Tobias and Murphey 1979; Westin 1979; Newland 1991), and are shared by many direction-coding sensory and motor systems (reviewed by Sparks et al. 1997). In such a "coarse-coded" system (Heiligenberg 1987), a single receptor does not uniquely encode direction. Instead, the ensemble activity of several receptors contains directional information that can provide for precise directional discriminations. Theoretical studies (Heiligenberg 1987; Theunissen and Miller 1991) suggest that the amount of directional information available from a population of coarsely coded receptors depends on how broadly tuned the individual receptors are and the positions of their response maxima within the range of stimulus directions. Simulations using four hypothetical mechanosensory interneurons with cosine-shaped directional tuning curves (Theunissen and Miller 1991) suggest that maximal transfer of directional information corresponds to equal (90°) spacing of the curves, with widths at half-maximum of 110°. Recordings from four interneurons in the wind-sensitive cercal system of crickets showed equal spacing and 130° half-widths, while the present recordings from crayfish primary mechanoreceptors correspond to a mean half-width of 122° (Eq. 2). These similarities are not surprising, given that both experimental datasets were obtained using non-saturating, suprathreshold stimulus amplitudes. Changes in stimulus amplitude or speed, however, can modify the shapes of receptor tuning curves (see Fig. 3B). Because excessively broad or narrow tuning curves will diminish the quality of the pooled directional information, it would be worthwhile to investigate whether gain-controlling mechanisms (cf. Burrows and Matheson 1994) act at some level to stabilize directional tuning properties.

Integration of directional information in the terminal ganglion (G6)

Both spiking and non-spiking mechanosensory interneurons in G6 exhibit directionally selective responses to mechanosensory stimulation of the tailfan (cf. Wilkens and Larimer 1972; Tautz and Plummer 1994). Primary mechanosensory interneurons have input from a variety of sources, including convergent inputs from directionally similar afferents (Wiese et al. 1976), inputs from separate ipsilateral nerve roots (Flood and Wilkens

1978), and contralateral, inhibitory inputs (cf. Schultz and Wilkens 1988). Beyond the expected pooling of excitation from ipsilateral, directionally similar afferents with inhibition from contralateral, directionally dissimilar inputs, additional insights into directional information processing in the crayfish are provided by comparisons with an analogous insect system. In the wind-sensitive abdominal cercal system of the cricket *Acheta domestica*, directional information from the filiform hairs is represented as a linear map in the terminal ganglion (Jacobs and Theunisson 1996). Although there is extensive overlap among the terminal arborizations of afferents having different preferred directions, the centers-of-mass of their projection patterns form a curvilinear, spiral-shaped map. In the crayfish, information on the morphology of tailfan afferent projections is limited mainly to mass forward fills of individual nerve roots (Calabrese 1976; Kondoh and Hisada 1986, 1987; Schmitz et al. 1993a). Although each root shows a distinct 3-D projection pattern, there is extensive overlap with terminals from other sensory nerve roots (Kondoh and Hisada 1987). Since the afferents within each root have a variety of preferred directions (see Figs. 6, 7), the observed overlap does not preclude a cricket-like spatial organization of directional information. In both systems, however, the hair-bearing appendages are moveable, suggesting that proprioceptive inputs (Goldstein and Camhi 1988; Field et al. 1990) are also important for directional information processing. In crayfish, stimulation of the tailfan chordotonal organs produces presynaptic inhibition near the terminals of as yet-unidentified tailfan hair mechanoreceptors (Newland et al. 1996), suggesting that these proprioceptors may indeed modulate a directional map.

Possible functional roles of filiform receptors in aquatic crustaceans

The multidirectional information provided by the tailfan receptors in crayfish suggests an important role for the tail as a general-purpose hydrodynamic sensor in long-bodied decapod crustaceans. Such a role is supported by experiments demonstrating specific behavioral responses to directional hydrodynamic stimuli, albeit without distinguishing among receptor types or restricting stimulation strictly to the tailfan. River-dwelling crayfishes (Maude and Williams 1983) and blinded Norway lobsters (Newland et al. 1988) orient themselves upstream or downstream in a flow tank, and spiny lobsters orient similarly to tidal currents in the field (Walton and Herrnkind 1977). In each case, however, the lowest effective current velocities were at least one to two orders of magnitude above the threshold for similar reactions in *P. clarkii* (1 $mm \cdot s^{-1}$; Ebina and Wiese 1984). In otherwise still water, small water jets directed at the tailfans of *P. clarkii* (Schmitz 1992) and the spiny lobster, *Panulirus argus* (Wilkens et al. 1996) elicit antennal movements, and similar attentive responses are elicited by the swimming movements of potential fish prey (Breithaupt et al. 1995). In contrast with these responses to near-field hydrodynamic stimuli, the tailflip escape response is elicited mainly by strong tactile stimulation (reviewed by Krasne and Wine 1984).

Most of the potential functional roles discussed above are characterized by relatively brief stimulation, and may involve filiform as well as other types of mechanoreceptors. Because of their tonic responses and non-adapting properties, however, filiform hair receptors may be particularly well-suited for monitoring steady or chronic hydrodynamic stimuli such as those associated with flowing water and wave surge along shorelines (Rudloe and Herrnkind 1980). Although *P. clarkii* itself mainly inhabits open, marshy areas with little or no dependable water flow, macruran decapods as a group occupy a variety of river, estuarine and marine habitats where water currents and oscillatory motions can provide predictable cues for orientation or navigation. For river-dwelling organisms, upstream rheotaxis has clear advantages for locating suitable habitat (Momot 1966) as well as for finding food or mates using both olfactory and hydrodynamic cues. Many crustaceans also monitor their orientation relative to the shoreline (Herrnkind 1983), information which can be crucial for choosing an appropriate direction in which to flee an approaching predator. Whereas celestial visual cues have often been implicated in this behavior (e.g., Goddard and Forward 1989; 1991), there is also evidence for the involvement of hydrodynamic receptors in the absence of visual cues (Walton and Herrnkind 1977; Nishimoto and Herrnkind 1978; Nevitt et al. 1995). Our results suggest that responses pooled from tailfan filiform hair receptors in *P. clarkii* are well suited for measuring directions of very small horizontal water displacements. Moreover, in crayfishes and other decapods, filiform hair receptor inputs from the tailfan are complemented by additional filiform sensilla located elsewhere on the body (Solon and Kass-Simon 1981; Bush and Laverack 1982). Thus, in conditions where visual cues are insufficient, many decapods may be able to rely upon filiform mechanoreceptors for orientation to water currents and to shorelines.

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