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A COMPARISON OF NEURONAL AND BEHAVIOURAL THRESHOLDS IN THE DISPLACEMENT-SENSITIVE PATHWAY OF THE CRAYFISH *PROCAMBARUS*

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SUMMARY

1. Velocity thresholds of neurones in the displacement-sensitive pathway of the crayfish were investigated using a stimulus programme of ramp fluid movements, with a range of velocities from 0·01–55 cm s^{-1} at the source (in both forward and backward directions).

2. The velocity of the stimulus was calculated to produce particle movements with velocities of between 0·001–1·0 cm s^{-1} at the receptors of the telson.

3. The distribution of threshold values for afferents in the fourth root of the sixth abdominal ganglion and interneurones of abdominal 4–5 connectives was plotted. Thresholds were similar for afferents and interneurones, differing in absolute value from 0·001–1·0 cm s^{-1}. Although neurones had threshold values throughout this range, there were peaks in the distributions. For the sample of 143 interneurones these were at 0·002–0·004, 0·01–0·08, 0·1–0·4 cm s^{-1}. In the sample of 43 afferents the middle peak fell at 0·02–0·06 cm s^{-1}, but the other two were the same as those for the interneurones.

4. The threshold for a behaviour pattern which makes crayfish turn to face the water current was around 0·1 cm s^{-1} continuous fluid speed.

5. Escape behaviour elicited by pure displacement stimuli was observed in our experiments only in animals of 2–3 cm body length which responded to displacement amplitudes of 28 mm s^{-1} and 6·7 cm s^{-1} maximum particle velocity.

6. Strongly phasic interneurones in the pathway obviously contribute significantly in triggering escape and need high acceleration transients to become fully active.

INTRODUCTION

Few neuronal circuits have been more thoroughly studied than the one mediating the highly modifiable escape response in crayfish. Following the work of Wiersma,

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Ripley & Christensen (1955) on the central representation of the sensory input from hairs stimulated by water displacement, numerous investigators have analysed synaptic connections between afferents and interneurones in the pathway (for reviews see Kennedy, 1974; Wine & Krasne, 1982).

Focusing on the synaptic connections between individual elements in the circuit has proved most successful: much is now known about the flow of activity from the receptors to the lateral giant fibre (LG), the trigger neurone for the motor command of escape (Zucker, Kennedy & Selverston, 1971; Zucker, 1972) so that we are now in a position to ask quantitative questions about how the circuit analyses naturally-occurring water movements.

The releasing stimulus in the pathway is the activation of dually innervated hair type sensilla on the exoskeleton by fluid movement (Mellon, 1963; Wilkens & Larimer, 1972; Wiese, 1976). Hair type sensilla are sensitive to both the displacement and velocity components of movements of the medium (Laverack, 1962; Wiese, 1976; Tautz & Markl, 1978; for theoretical considerations see Markl, 1973; Tautz, 1979). The measurements of Tautz & Sandeman (1980) on the sensilla of the chelae in *Cherax* have shown the dependence of the threshold on the component of acceleration.

To begin the analysis we scanned threshold sensitivities of the neurone types involved to a defined stimulus parameter with the intention of learning about the organization of the pathway from the arrangement of thresholds. Smooth ramp-type movements of a sphere (dipole source) were used as the experimental stimulus because they approximate the displacements generated by moving animals and the interneurones are less likely to habituate rapidly to them. Using such experimental conditions we have measured thresholds of afferents and interneurones to particle velocity and have compared these thresholds with those for two types of behaviour naturally elicited by water movements: orientation towards water current and the escape response.

METHODS

Specimens of *Procambarus clarkii* from Monterey Bay Hydroculture Farms POB 434 Soquel CA 94073 U.S.A., measuring 6–8 cm in body length, were used for the isolated tailfan preparation. This dissection has been described repeatedly (e.g. Calabrese, 1976).

A total of 34 animals were used in the reported experiments. Suction electrodes served to record from afferent axons in the fourth root of the sixth abdominal ganglion (G6) and from interneurones near the ventral surface of the desheathed connectives between abdominal ganglia 4 and 5, both *en passant* and from fibre bundles cut anteriorly. To prevent repetitive recording from the same neurone, not more than six units were tested at one recording site at the root or at the connective. Mostly, the electrodes were moved in addition to record from fibres of the contralateral root and connective. A stimulus movement monitor and the neurone responses were stored on magnetic tape, sections of which were later photographed. To reduce stray activity generated by constant oscillations of the fluid surface, we took advantage of the fact that such oscillations are attenuated strongly with increasing depth (see e.g. Wiese,

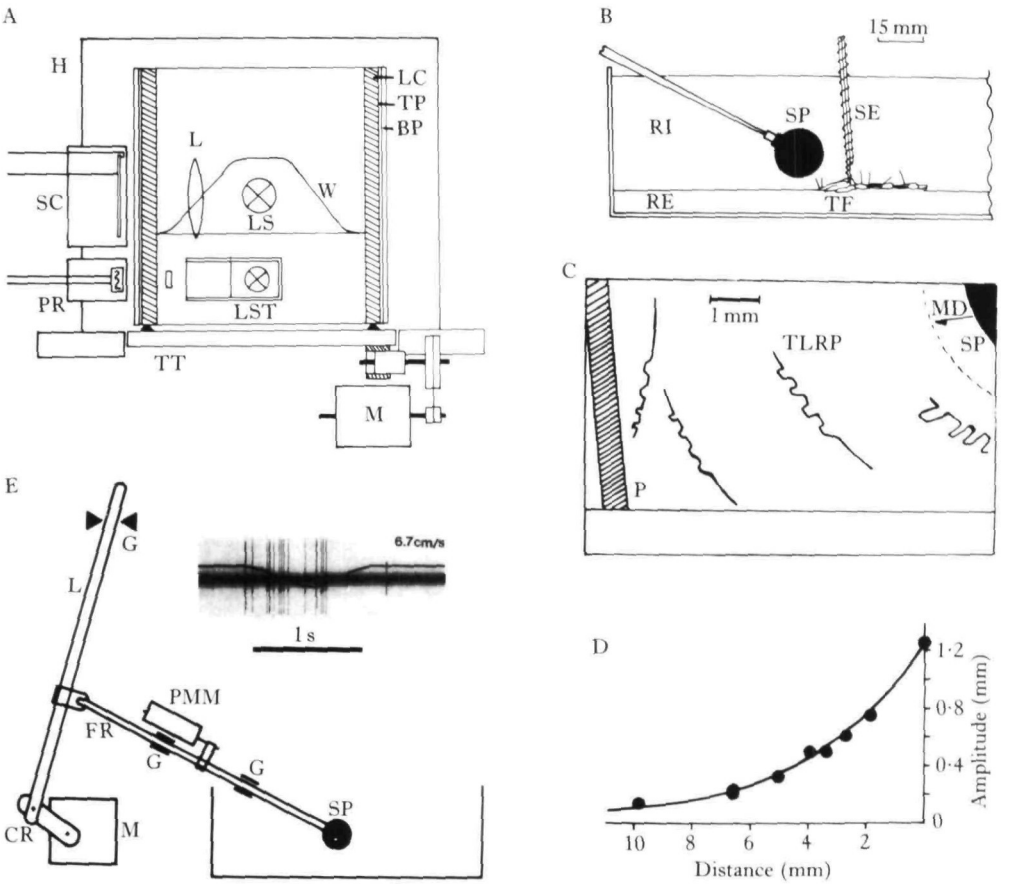


Fig. 1. Experimental arrangement and conditions. (A) Opto-mechanical generation of ramp-type stimuli and a stimulus programme. A Lucite cylinder (LC) on a turntable (TT) rotates at selected, calibrated speeds. It carries a mantle of transparent paper (TP) covered by a mask of black paper (BP) into which a series of four trapezoid windows (W) have been cut. A faint light (LS) inside the drum shines through this window and through a slit diaphragm of 1 mm width to illuminate a solar cell (SC) which produces an electrical signal describing the contour of the window. A trigger pulse at the onset of the stimulus programme is similarly generated by a light source (LST), a tiny window in the black paper and a photoresistor (PR). H, hood; M, motor; L, lens. (B) Configuration of the isolated tailfan (TF), mounted on a layer of elastic resin (RE), and the stimulus, a fluid-displacing sphere (SP). The experimental chamber is filled with Ringer (RI) and a suction electrode (SE) is adjusted to record either from afferent axons in the roots of ganglion 6 or from interneurones in the connectives between ganglia 4 and 5. (C) The track of light reflecting particles (TRLP) as they are displaced by the sphere (SP) moving in the pattern of the stimulus programme. The displacement becomes smaller with increasing distance from the sphere. P, visual marker (pin); MD, movement direction. (D) Direct measurements of particle displacement amplitude at several distances from the surface of the sphere, made with a high power, calibrated dissection microscope. (E) The mechanical system used for generating large amplitude movements. The same sphere (SP) used in the other system is moved by a long flexible rod (FR) which is supported by two guides (G). The motor (M), which stops automatically after each turn, moves a lever (L) by a crank (CR). Rod and sphere movements are monitored by a linear potentiometer (PMM). Inset: neuronal discharge evoked by this stimulus movement shows that sphere movements, not artifacts at start or stop, are the effective stimuli in this configuration.

Wollnik & Jebram, 1980) and mounted the tailfan and the attached ventral cord in a dish 20 × 9 × 6 cm and covered by a 5 cm deep layer of van Harreveld (1936) solution. Temperature in the bath was kept at 15 °C.

Control of stimulus movement

Particle displacements with velocities ranging from less than 1 mm s^{-1} up to 55 cm s^{-1} were generated by movements of a plastic sphere (dipole source) of 16 mm diameter driven by the opto-electric function generator described in Fig. 1A. The most important properties of this device are the reproducible production of a defined set of fluid movement stimuli with special care taken while cutting the stimulus contour window to avoid transients at the onset of movement. From the correlation between response amplitude and movement velocity seen in the units of Fig. 2A, from the occurrence of responses only in higher velocity stimuli and from the latency of response with respect to onset of movement, which often exceeds 40 ms (see Fig. 2B: time calibration 2 s), we believe the response is to the stimulus movement rather than to any possible transient click at the onset.

The gradual attenuation of particle movement with increasing distance from the sphere was studied by photographing reflecting dust particles in the fluid during the stimulus programme. Direct visual measurement of attenuation at steps of 1 mm from the surface of the sphere was made by observation with a high power calibrated dissecting microscope (Fig. 1B, C, D).

The stimulus programme consisted of four approximately square waves which differed from each other by the increasing slope speed of the ramp-rise. Intermediate values of ramp velocity were obtained by rotating the programme drum (Fig. 1A) at three preselected speeds.

In addition we constructed a device to generate large amplitude displacements (Fig. 1E). This crank and lever mechanism produced fluid speeds of 4–12 cm s^{-1} when the sphere was moved through 2·8 cm.

Behavioural tests

Orientation turns toward the water current

An oval channel built from Lucite with total dimensions of 60 × 40 cm and a cross section of 5 × 5 cm was used (Fig. 4). Steady fluid movements, in either direction, ranging from 0·05–2·0 cm s^{-1} were produced by a submerged miniature pump which could rotate at several controlled speeds. Coarse rubber foam blocks within the channel provided an additional means of slowing the water movement when necessary.

Three to six specimens of crayfish of 2–3 cm body length were placed together in a screened compartment of the channel in still water. They were allowed to adapt to the surroundings for 10–20 min. When the pump was switched on, the number of animals facing the current was counted. Similar counts were repeated at 10-s intervals. About 20 s after the flow speed had reached a steady state, the animals lost interest in the stimulus and started other activities. Fluid direction was regularly reversed to check for directional preferences. Darkroom illumination reduced the influence of visual inputs.

Triggering escape behaviour

The crank and lever mechanism was used to test escape responses of individual specimens of 2–3 cm body length by bringing the sphere in from the rear so that it just cleared the tailfan.

RESULTS

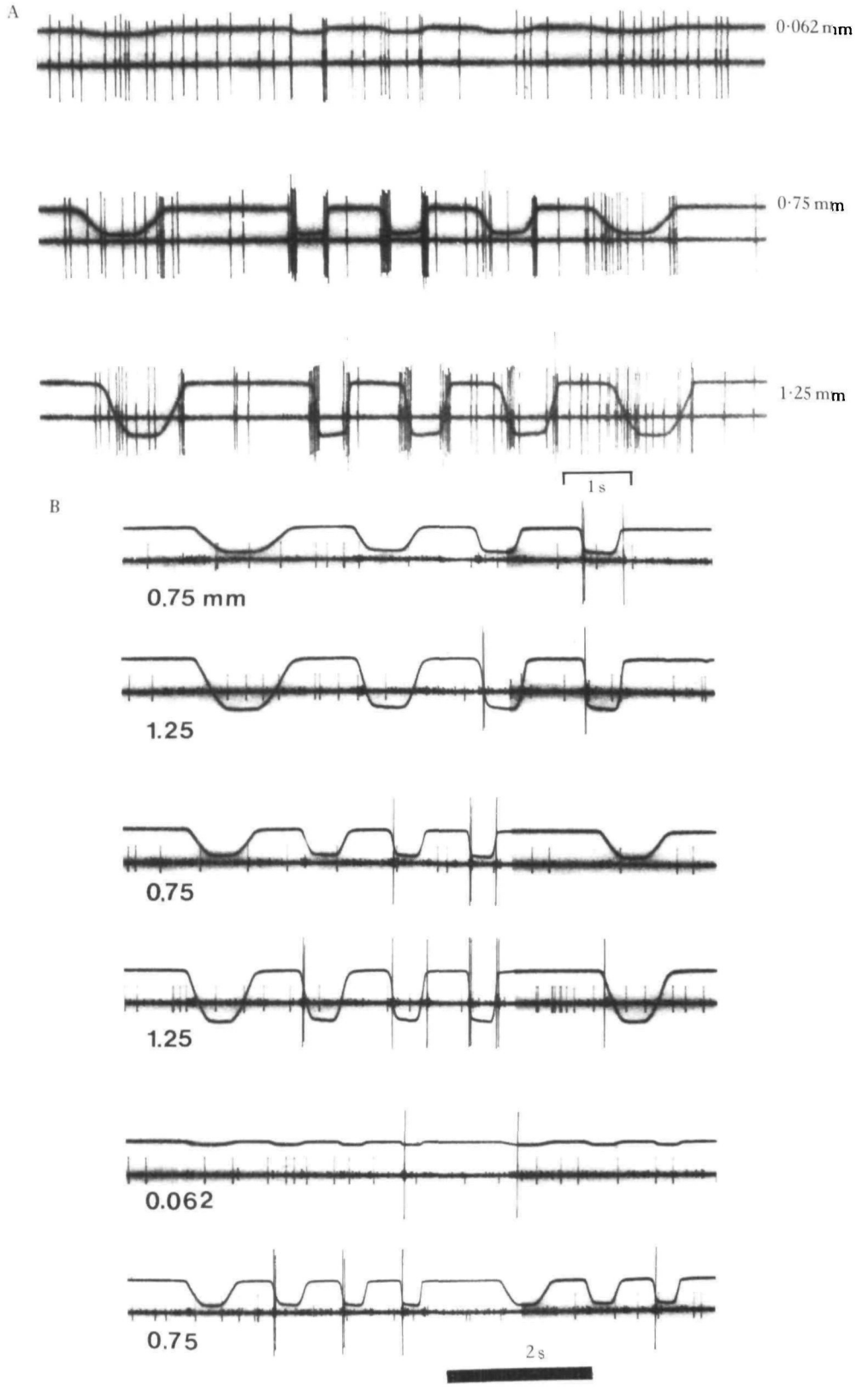
Velocity thresholds of afferents and interneurones in the displacement-sensitive pathway

The recorded neurones in the fourth root of the abdominal ganglion 6 (afferents) and in the 4–5 connective (interneurones) of the abdominal nerve cord responded to movements of the sphere in two distinct ways: type I neurones were extremely sensitive and their impulse frequency in response to suprathreshold movements was easily modulated (Fig. 2A). Type II neurones, which usually had larger spike amplitudes in extracellular recordings, seldom produced more than one spike per stimulus movement, even with large amplitude stimuli (Fig. 2B). This distinction applies to both afferents and interneurones.

Data of Wiese & Schultz (1982, their Fig. 4) indicate that the latency of interneurone response in this pathway is usually about 40 ms, including the time required for the surface wave stimulus to develop and travel to the site of the receptors. Some of the latencies of the responses seen in Fig. 2B exceed this amount of time significantly; this latency increase, besides being attributable to the threshold condition speaks against artifacts at movement onset as the effective stimulus. However, the latencies observed are not large enough clearly to separate between velocity and acceleration components in the stimulus and their individual effect on the response.

The water movements generated were always directed along the longitudinal axis of the tailfan preparation. Earlier work (Wiese, Calabrese & Kennedy, 1976) has shown that the majority of interneurones in this pathway is directional. The directional sensitivity arises from the two afferents which innervate each hair sensillum, one sensitive to headward, the other to tailward movements of the medium (Wiese, 1976). This dualism is maintained at the level of the interneurones, which form two populations with opposite polarities. In the sample recording of Fig. 2A little directional selectivity is seen, except that on close observation the impulses seen to respond to one movement direction are of slightly different size than the ones reacting to the other direction and thus may represent a different neurone. In Fig. 2B the neurone is responding to both movement directions, however a preference to one direction is obvious.

Fig. 2. Stimulus programme and neuronal discharges. (A) A high sensitivity interneurone in the connective between abdominal ganglia 4 and 5. Displacement amplitude values are shown on the right. Time bar: 1 s. (B) Record from a very phasic interneurone in an experimental series where stimulus amplitude (velocity) was changed by varying the sphere displacement and ramp speed. Values on the left give sphere displacements. Velocity can be calculated. Downward deflection of the movement monitor trace represents movement of the sphere towards the tailfan. The threshold of the large phasic unit in this record is 0·15 cm s^{-1}. The top record shows responses to the slowest speed at which the programme was presented and the bottom record responses to the fastest speed at which the Lucite cylinder could revolve. Time bar: 2 s.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A few interneurones, in particular the lateral giant (LG) and interneurone A6/A/6A1 (nomenclatures from Wiersma & Hughes, 1961; Zucker, 1972; Sigvardt, Hagiwara & Wine, 1982, respectively) respond to movements in both directions, although with differing sensitivity (Wiese *et al.* 1976; Fig. 5).

Velocity thresholds at the site of the receptors were read from a curve describing attenuation of particle displacement with distance from the sphere surface (Fig. 1D). Distances from the sphere surface to the centre of the fourth root receptive field were measured from photographs taken at the end of each experiment.

Neurones with thresholds at velocity values between 0·001 and 1·0 cm s^{-1} were found, with the histogram of encountered thresholds (Fig. 3) showing data from 43 afferents and 143 interneurones. Peaks in the distribution of thresholds appear at about 0·002 and between 0·1 and 0·2 cm s^{-1}. The interneurones have a third peak between 0·01 and 0·04 cm s^{-1}. A corresponding third maximum in the distribution of afferent thresholds is less distinct.

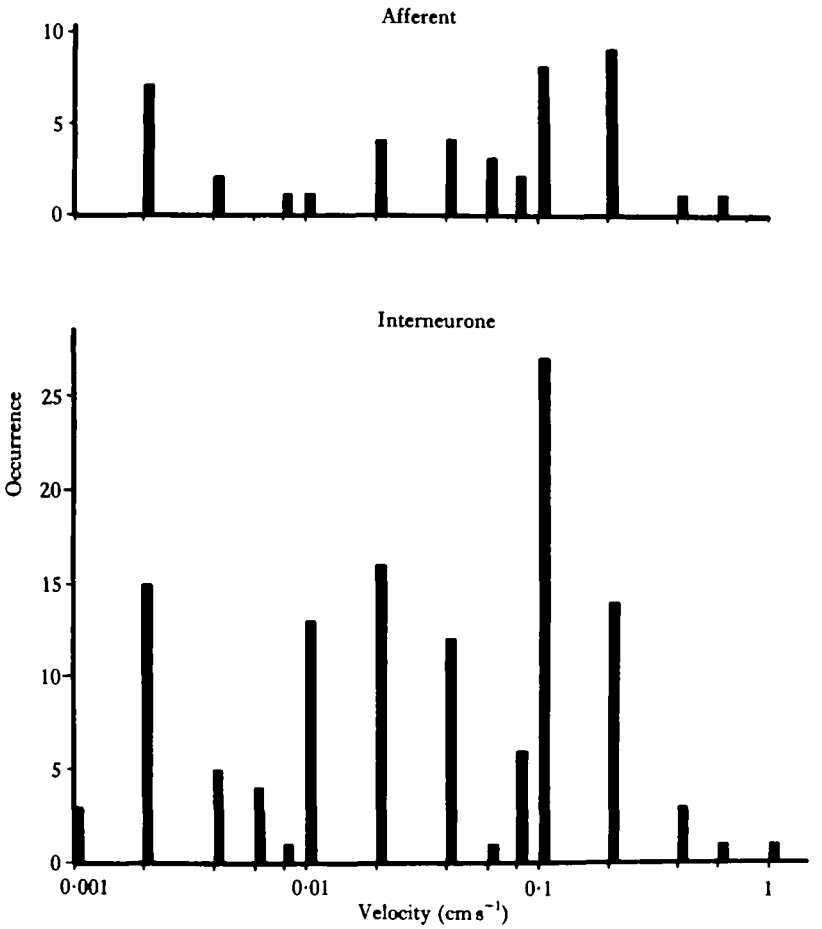

Fig. 3. Histograms of velocity thresholds for all the 43 afferents and 143 interneurones recorded. The ordinate gives the number of times a certain threshold value occurred; the abscissa gives velocity values corrected for the receptor sites on the tailfan. Each decade was divided into 5 bins; (bin width, 0·2 units).

To avoid repetitive recording from the same interneurone the recording sites were as far apart from each other as possible (including changes from left to right connective) and the response characteristics of the encountered neurones were carefully observed.

Velocities of more than $1{\cdot}0\,cm\,s^{-1}$ at the site of the receptors in our experiments were not observed to recruit additional afferents and interneurones either of type I or type II responses. We tested this by moving the vibrating sphere closer to the preparation than usual, producing about $10\,cm\,s^{-1}$ in velocity at the site of the receptors, but nothing but sharp clicks seemed to trigger more afferent elements.

With a centre frequency of 20 Hz of a stimulus event and 1·25 mm movement amplitude of the sphere, the $1{\cdot}0\,cm\,s^{-1}$ stimulus at the site of the receptors had an approximate acceleration of $160\,cm\,s^{-2}$. (The exact value of acceleration could only be obtained by direct measurement.)

The threshold value of the large size unit responding in Fig. 2B is located between the margins 0·08 and $0{\cdot}15\,cm\,s^{-1}$. On the basis of the extraordinary size of its extracellularly recorded action potentials, which is a sign of considerable fibre diameter (compare cross section of ventral cord in *Procambarus* with identified interneurone A: Zucker, 1972) and on the basis of the rare sensitivity for fluid movements in both principal directions with higher sensitivity in one than in the other (Wiese *et al.* 1976) we assume that this interneurone in Fig. 2B is Zucker's interneurone A, identical with A6 of Wiersma & Hughes (1961), an interneurone segmental in nature and electrically coupled to the lateral giant LG.

Thresholds of behaviour triggered by displacement stimuli

A distribution of afferent and interneurone velocity thresholds which shows distinct peaks in the histogram and with the peaks spaced apart about 1 log unit suggests the existence of sensitivity levels within this sensory pathway. The significance of such levels can only be demonstrated by relating them to the thresholds for release of types of behaviour initiated by water displacements.

One such behaviour pattern, the turning of the animal to face the water current, is released by comparatively slow water movements. Fig. 4 summarizes the measurements of threshold water velocity required to make small baby crayfish (2–3 cm) perform the orientation turn. The probability plots show that no positive response to the movement stimulus is detectable below $0{\cdot}1\,cm\,s^{-1}$. This figure appears to be low at first sight, but in the band-width of thresholds encountered the figure represents the upper half of values. What then is the nervous system doing in this context with the activity not leading to motor output?

We have also tried to evoke escape responses by using a larger calibrated displacement produced by the apparatus shown in Fig. 1E. A crank and lever mechanism driven by a motor that stops automatically after each turn moved the 16 mm sphere with a peak-to-peak amplitude of 28 mm and a peak velocity of $6{\cdot}7\,cm\,s^{-1}$. At this stimulus setting, no crayfish of 6–8 cm body length was ever induced to perform a tailflip response. However, the smallest crayfish available at that time, of 2–3 cm body length, and adapted for 15 min to the container, responded without exception to the stimulus.

All observers of crayfish behaviour agree that baby crayfish are much more active

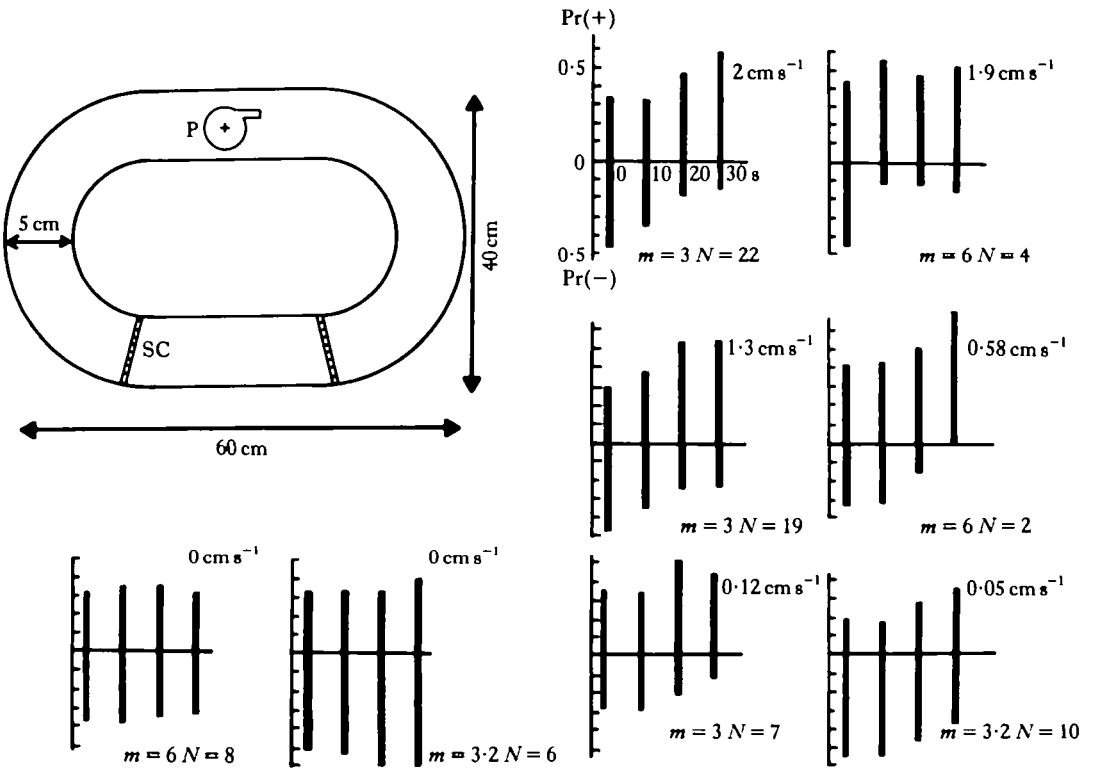

Fig. 4. Determination of thresholds for the orientation response. The test chamber is an oval channel 60 × 40 cm with a cross-section of 5 × 5 cm. A submerged pump (P) drives the water at calibrated speeds in either direction through the channel. The baby crayfish to be tested are confined by the two screens (SC). The bar-graphs show the ratio of crayfish orientating towards the flow (Pr+) to the total number of animals in the screened compartment. Four counts were made at 10-s intervals from starting the pump (0 s). *m*, average number of animals in trial; *N*, number of trials performed. Flow direction is regularly reversed to exclude directional preferences. The results show a threshold at 0·1 cm s^{-1} for this orientation response.

and mobile than adult specimens. On the other hand, one would expect that with increasing body surface a larger number of sensilla become incorporated into the sensory system. *De facto* however our attempts to trigger escape in adult crayfish by pure displacement stimuli failed, and we have to assume that the corresponding threshold is still far above the stimulus amplitude employed here.

At present the question is open whether the observed threshold increase in adult *versus* young specimens is due to the probable increased diameter of the lateral giant fibre in a larger crayfish (additional membrane area means additional load in the depolarizing process), or to better motility of sensilla in young animals, or to additional inhibitory circuits damping LG activity in the fully-developed circuitry. The most promising cue however, which will be discussed in detail below, is drawn from the observation of Wine & Krasne (1972) that it takes pinching of abdominal pleurites in *Procambarus* to repeatedly evoke escape responses. This suggests that the fluid

displacement stimulus may not reach an important section of the population of mechanosensory afferents driving the lateral giant fibre.

DISCUSSION

To measure sensitivity in neurones responding to fluid displacements, we have designed a stimulus programme generator producing a single-ramp function (Fig. 1A), which should reduce interference from habituation to a minimum. Using this stimulus programme, both afferents and interneurones were found to have velocity thresholds between 0·001 and 1·0 cm s^{-1}. Although tests were carried out with the receptors in the proximity of the vibrating sphere (maximum velocity of the sphere 55 cm s^{-1}), no units with thresholds higher than 1·0 cm s^{-1} were found. In contrast to our expectation, an orientation behaviour had a threshold at the upper end of this neuronal threshold range and the tailflip response was very difficult to elicit at all. Two questions are raised by these results, firstly the significance of the neurone thresholds for the organization of the sensory pathway and, secondly, the apparent mismatch between neuronal and behavioural thresholds.

Neuronal thresholds and the organization of the sensory pathway

There are two possible ways in which a range of thresholds for sensory stimulation can be achieved. The receptor population may have a uniformly high sensitivity with interneurones solely responsible for stimulus amplitude detection. Alternatively, both afferents and interneurones could have equally heterogeneous threshold values with the most sensitive receptors responsible for the sensitivity of the most sensitive interneurones.

The advantage of using the latter arrangement, which is the case in this system, may lie in the improved capability to encode a wide dynamic range of stimuli and to focus on different parameters of the stimulus. The sensitivity of receptors to fluid displacements is clearly related to receptor morphology; additionally graded synaptic efficacy of synapses between distinct afferents and certain interneurones introduces the possibility of regulating the contribution of receptors with characteristics matched to stimulus parameters to the activity of interneurones.

The morphology of hair-type receptors on the crayfish telson (Wiese, 1976) and chelae (Laverack, 1962; Tautz & Sandeman, 1980) ranges from short unfeathered rods, 0·2 mm long, to thin, elongated feathery shafts and antenna-like sensilla over 1·0 mm long (Wiese, 1976). Tautz (1979) shows that the hinge at the hair base generally has very limited freedom of excursion and is easily overloaded. Consequently, if receptors are to respond to both low and high amplitude movements, a range of hair lengths is required and a corresponding range of thresholds is to be expected.

In addition, Kennedy (1974) reports that the efficacy of connections between afferents and interneurones in the pathway for fluid displacement varies from one sensory cell to the next. The most effective connections are made by the afferents from the small inconspicuous hairs on the front edge of the telson; the sensory cells of these sensilla are extremely phasic and were often observed to fire at the moment of contact with the tip of the paintbrush; stimulation of such phasic receptors, also driven by vibrations propagating along the body skeleton, is very likely to release an escape

response, because they make highly efficient contacts with interneurone A and the LG.

With Wine & Krasne (1972) reporting that direct touch and even pinching were the most effective stimuli releasing escape, it is now rather obvious that by using pure displacement stimuli we have systematically excluded all the more phasic receptors of the population, the activity of which is important in boosting activity in the interneurones such as the LG fibre.

Mismatch between neuronal and behavioural thresholds

Why then does the threshold for the orientation turn towards the water current lie at the upper end of the range of thresholds found in interneurones while apparently neglecting more sensitive inputs?

Reichert *et al.* (1982) and Wiese & Schultz (1982) have observed that a contrast-enhancing lateral inhibitory circuit within the displacement-sensitive pathway constitutes a powerful common mode rejection mechanism. Similarly patterned large scale water movements, such as steadily flowing water, are neuronally suppressed to keep the pathway sensitive to small, local displacement signals generated either by our vibrating sphere or by live prey or attackers. Reichert *et al.* (1982) found that local interneurones, directional selective and inhibitory (LDS), are the responsible producers of common mode rejection. It may be this mechanism that raises the threshold of the orientation turn towards the water current as compared to the neuronal thresholds observed in our experiment with the small local displacement signal.

Moreover, strong lateral inhibitory interconnections from segment to segment of the body have recently been demonstrated (Wiese & Wollnik, 1983) in this sensory system. The significance of lateral inhibition for extending the dynamic range of a pathway has been shown by Palmer & Evans (1982) in the cat cochlear nucleus. They found that inhibitory interactions elicited by bandstop noise (noise consisting of both higher and lower frequencies than the test tone) enabled a set of second order interneurones to cover almost the entire dynamic range of the auditory pathway (4–5 log units). Without these interactions the same neurones were barely able to code 2 log units of sound pressure level.

If lateral inhibition between frequency bands is transformed in lateral inhibitory action between receptive fields and the connected interneurones, then it is well imaginable that damping by inhibitory circuits, especially in the intact animal, keeps activity in key interneurones at moderate levels and results in spikes in the LG occurring only during stimuli containing high acceleration components.

Experience might also induce the crayfish not to move before the very last second; because in a dense medium like water, movements cause water displacements which again tell predators about the presence of prey.

Patterns of behaviour, like escape, are elicited at the upper end of the dynamic range in a pathway. Orientation turns in response to gross fluid movements on the other hand are not necessarily identical in threshold with the threshold of perception of particle displacement, which has been carefully measured in lobsters (Offutt, 1970). Monitoring changes in heart rate after conditioning the animals to a displacement stimulus demonstrated a maximum sensitivity of perception at 75 Hz and $0{\cdot}7 \times 10^{-4}\,\mathrm{cm\,s^{-1}}$. This velocity value is a factor of 10 lower than the lowest thresholds

encountered in interneurones in the present study. This difference could be due to the existence of more sensitive receptors than the ones encountered on the tailfan. As another possibility, sensory convergence has to be mentioned; this cannot take effect in recordings from individual interneurones with input from the isolated tailfan only.

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