J Comp Physiol A (1995) 177: 781–791

ORIGINAL PAPER

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The role of touch, pressure and nociceptive mechanoreceptors of the leech in unrestrained behaviour

Accepted: 9 May 1995

Abstract 1. The maximum force exerted against an isometric force transducer by 6 leeches weighing 2.6–3.7 g, as they squeezed through apertures of different widths varied inversely with aperture width.
2. T cells in the leech skin code for velocity of indentation, not pressure or displacement. The frequency with which T cells fire is best described by two log functions, one for low, another for fast indentations. T cells responded to indentation velocities down to 10 $\mu m\,s^{-1}$.
3. The average threshold pressure for 5 P cells was 150 kPa and for 5 N cells was 521 kPa.
4. We conclude from these data that when leeches explore their mechanical environment and initiate contact with external objects, the threshold pressure for N cells is rarely crossed. Of the three classes of mechanoreceptor, T cells are the main modality through which leeches obtain contact information, though P cells may occasionally be recruited for local pressure peaks.

Key words *Hirudo medicinalis* · Skin · Pressure · Velocity · T P N cells

Introduction

In order to make appropriate behavioural decisions animals have to obtain information about their immediate environment. For this task leeches are equipped with a number of exteroreceptors which include eyes (Lasansky and Fuortes 1969; Kretz *et al.* 1976; Petersen 1983), segmental photoreceptors (Kretz *et al.* 1976) chemoreceptors (Elliott 1985, 1986), water movement receptors (Friesen 1981; Gascoigne and McVean 1991) and skin mechanoreceptors (Nicholls and Baylor 1968). Mechanical stimulation of the skin elicits immediate and repeatable behavioural responses. Gee (1913) showed that touching the skin on the anterior part of the body of the leech *Dina microstoma* with a flexible hair bristle induced it to turn away from the point of contact. Touching the posterior end produced looping or, if the leech was more active, swimming. Gee (1913) also showed that the response changed with the intensity of the stimulus. A stronger stimulus increased the amplitude of the turn, while a "stimulus of yet greater intensity" caused the leech to reverse the direction of movement and swim.

These early and careful observations were the prelude to work which sought to determine the neuronal basis by which these behaviours were selected and executed (Kristan et al. 1982; Friesen et al. 1978; Kristan 1982; Magni and Pellegrino 1978; Ort et al. 1974; Stent et al. 1978; Weeks and Kristan 1978; Lockery and Kristan 1990a, b; Weeks 1982a, b; Brodfuehrer and Friesen 1986a, b, c). A key paper by Nicholls and Baylor (1968) showed that different amplitudes of touch were detected by different categories of mechanoreceptors. The soma of each mechanoreceptor was shown to be located in the segmental ganglion and served ipsilateral skin in its own (Nicholls and Baylor 1968) and, via axons in each of the ipsilateral connectives, immediately adjacent segments (Yau 1976). Nicholls and Baylor (1968) showed that the three T or touch cells on each side of the ganglion responded when the skin was indented with a 20 μm diameter stylus with a force not exceeding 4.9 mN and adapted rapidly. Each of the two P or pressure cells responded when a larger stylus with a diameter of 200 μm was applied to the skin with a force of 68.7 mN and the two N or nociceptive cells fired when a force of 235.4 mN was applied with the same stylus. It was clear that the force applied to the skin which elicited responses from the P and N cells was above threshold in each case but no experiments were, or have been, carried out to determine the threshold of these mechanoreceptors. In

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subsequent accounts T cells have been considered to be mechanoreceptors which behave like the P and N cells but with a lower threshold. Thus Debski and Friesen (1987) describe the T cell as "being so named because it fires in response to a light touch of the body wall, the pressure or P cell fires when a slightly greater pressure is applied" and in a similar vein Kristan (1982) confirms that "low amplitude mechanical stimuli selectively stimulated the T cell without affecting the P cell" while "at higher stimulus intensities the P cell was activated".

Since T, P and N cells respond to mechanical deformation of the skin, the relationship between the activity of these cells and the response of the whole leech has been examined on a number of occasions. Kristan et al. (1982) confirmed Gee's (1913) observations, this time with *Hirudo medicinalis* and *Macrobdella decora*. These authors showed that there was no regional variation over the body in the threshold of electrical stimulation for P and T cells and concluded that the normal repertoire of behavioural responses elicted by touching the body wall was mediated through the activity of T and P cells. In subsequent experiments Kristan (1982) measured the strength of contraction of dorsal longitudinal muscle in response to intracellular stimulation of T and P cells and showed that P cells were significantly more effective in inducing muscle tension than T cells, although simultaneous T cell activity disproportionately increased the strength of contraction produced by a P cell. However, paired intracellular recording showed that T cell activity was more effective than P cell activity in depolarising the L cell, a motorneuron which innervates longitudinal muscle. Kristan (1982) attributed the stronger contraction induced by P cells to additional interneuronal pathways not activated by T cells.

Since Gee (1913) had shown that strong mechanical stimulation to the skin can induce swimming, Debski and Friesen (1987) used a similar approach to that employed by Kristan (1982) to measure the relative efficacy of T, P and N cells in eliciting swimming. It was known (Debski and Friesen 1985) that light stroking of a body wall flap attached to the ventral nerve cord evoked bouts of swimming activity. Debski and Friesen (1987) showed that intracellular stimulation of P and N cells at frequencies at or above 15 Hz induced fictive swimming in a significant number of preparations. T cells were effective only when excited in pairs. Debski and Friesen (1987) conclude that light stroking of a small portion of the body wall sèlectively stimulates three T cells and that this amount of excitation is enough to elicit swimming.

Brodfuehrer and Friesen (1986c) provided some insight into the route by which mechanical stimulation of these skin receptors influenced the swim generator by locating two cells, Tr1 and Tr2, in the suboesophageal ganglion which act as trigger cells for swimming and which, in turn, are excited by the mechanoreceptor cells. Both P and the medial N cells make monosynaptic connections onto contralateral trigger cells, though P cells evoke the strongest response. T cells are least effective.

The experiments described above make it clear that activity in T, P and N mechanosensory cells is capable of inducing avoidance and swimming behaviour in whole leeches or triggering neuronal patterns of activity in isolated CNS preparations, associated with swimming and avoidance, whether the mechanical stimuli have been applied to the skin or simulated by intracellular depolarisation of the mechanosensory cells. However, for much of the time leeches probably lie undisturbed or navigate their way through their environment without being attacked. The forces pressing against the skin will be those generated by the activities of the leech itself. In this paper we set out to try to answer the following questions: (1) what magnitudes of pressure might leeches normally expect against the skin as a result of their own activity and (2) do these pressures exceed the threshold pressures for the T, P and N mechanosensory cells?

Materials and methods

Animals

Adult medicinal leeches, *Hirudo medicinalis*, obtained from a commercial supplier, Ricarimpex, were kept in artificial pond water, changed weekly. Leeches were maintained at 12 °C in a reversed 12:12 h light dark regime.

Behavioural experiments

In order to measure the force leeches can exert against objects, they were persuaded to squeeze through a gap 19 mm wide whose aperture could be altered and measured. Leeches take enthusiatically to this challenge. The bottom of the gap was made of perspex sheet, the top of the gap consisted of a perspex probe, with a contact surface area of 19 × 1 mm. The probe itself was firmly braced by two low friction wheels held against the anterior and posterior face of the probe by two strong springs. These wheels minimised movement of the probe along the axis of the leech but allowed the probe to move easily in the vertical plane, resisted only by the springs inside the transducer. A 50 g weight applied to the probe along the axis of the leech (by a pulley arrangement) generated a movement of the probe which was 0.02 times the amplitude of the movement in the vertical direction when the same weight was applied vertically. The probe was attached to a Grass FT 103 force transducer. Stiff springs were used to make the transducer isometric, giving it a resistance of 1 Newton per 15 μm displacement. The transducer was clamped in a rigid (Palmer) stand so that it could be raised or lowered to alter the size of the gap. Gap sizes were set at 5, 4, 3, 2 and 1.5 mm. Care was taken to prevent the probe from touching the sides of vertical barriers forming the edges of the gap. Signals from the Grass transducer were amplified with a Neurolog NL 107 amplifier, stored on a Racal 4DS Instrumentation Recorder and subsequently analysed on a PC using a CED interface and Spike 2 analysis program. The transducer was calibrated with gram weights. In some experiments photographs were taken as the leech squeezed through the aperture to determine the area of the contact between the leech and the probe.

Electrophysiology

In order to determine whether T, P and N mechanosensory cells are excited by pressure amplitudes equivalent to those generated when squeezing through a narrow aperture, single ganglion-skin preparations were used. The skin and attached ganglion was pinned out on silastic rubber (Sylgard™) in a glass petri dish and perfused with standard leech Ringer (Muller et al. 1981). The soma of T, P and N cells ipsilateral to the skin were penetrated with glass microelectrodes filled with 3 *M* potassium acetate. Two probe sizes were used. Initially we used the same probe that had been used in the behavioural experiments to exert pressure against the skin. As before, the probe was attached to the Grass FT 103 force transducer. In later experiments a metal stylus with a circular foot of 500 μm diameter, was used. The small size of this probe considerably reduced movement artefact. In each case the probe-transducer assembly was held in a rigid stand and lowered in incremental steps onto the skin. In order to reduce movement artefact a groove was cut in the Sylgard down to the floor of the petri dish and the roots linking the skin to the ganglion stretched across the gap. We were also able to record the activity of T cells with extracellular suction electrodes on the ganglion sheath and thus confirm data obtained with intracellular electrodes. We were unable to record from P or N cells in this way.

The response of T cells to skin indentation at different velocities was determined by deforming the skin with the 500 μm diameter metal probe attached to the piston of a Derritron VP2 moving coil vibrator, driven by a power amplifier controlled by PC generated voltage signals. The displacement amplitude of the probe at the different velocities used in these experiments was measured with the Grass FT103 transducer, with a stiffness of 1 Newton per 5097 μm displacement. The amplitude of the voltage signal to the vibrator, used in the records to indicate probe position, was arithmetically adjusted to represent the correct displacement at all velocities used.

Stress-strain relationship of the body wall to indentation

A portion of body wall was pinned out onto a wax dish, which was in turn mounted on the piston of the moving coil vibrator. As before the movement of the coil was computer controlled. The wax dish was driven vertically, at a predetermined speed, so that the stationary probe attached to the Grass force transducer, indented the skin. Probe displacement was previously measured in response to calibrated weights, so that the voltage generated by the Grass transducer could be used to measure both force and distance through which the transducer had been moved by virtue of pressing against the skin. The transducer was isometric as before, with a resistance of 15 $\mu m\,N^{-1}$.

Results

Forces exerted by leeches as they squeeze through a constriction

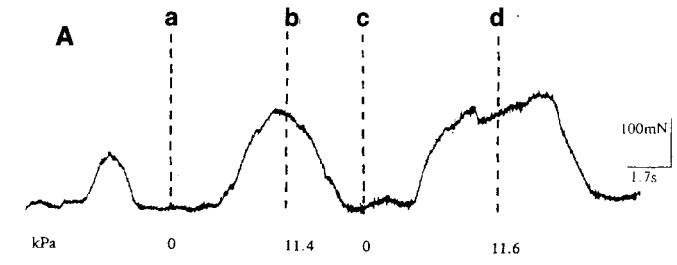
Six leeches, weighing between 2.6 and 3.7 g were induced to squeeze through a gap between a probe attached to a force transducer and the floor of the experimental chamber. The aperture was varied, in 1 mm steps, between 2 and 5 mm. All six leeches were able to repeatedly get through slits of these dimensions. As Fig. 1 shows, the force exerted against the probe varied cyclically as waves of contraction passed along the body. As the aperture was reduced the maximum force exerted increased monotonically (Fig. 2). None of the leeches were able to penetrate a gap of less than 2 mm, although some individual leeches squeezed the anterior portion of their body through the aperture and then retreated. We measured the width of the leech within the gap and used this measurement to convert the vertical force exerted into pressure units.

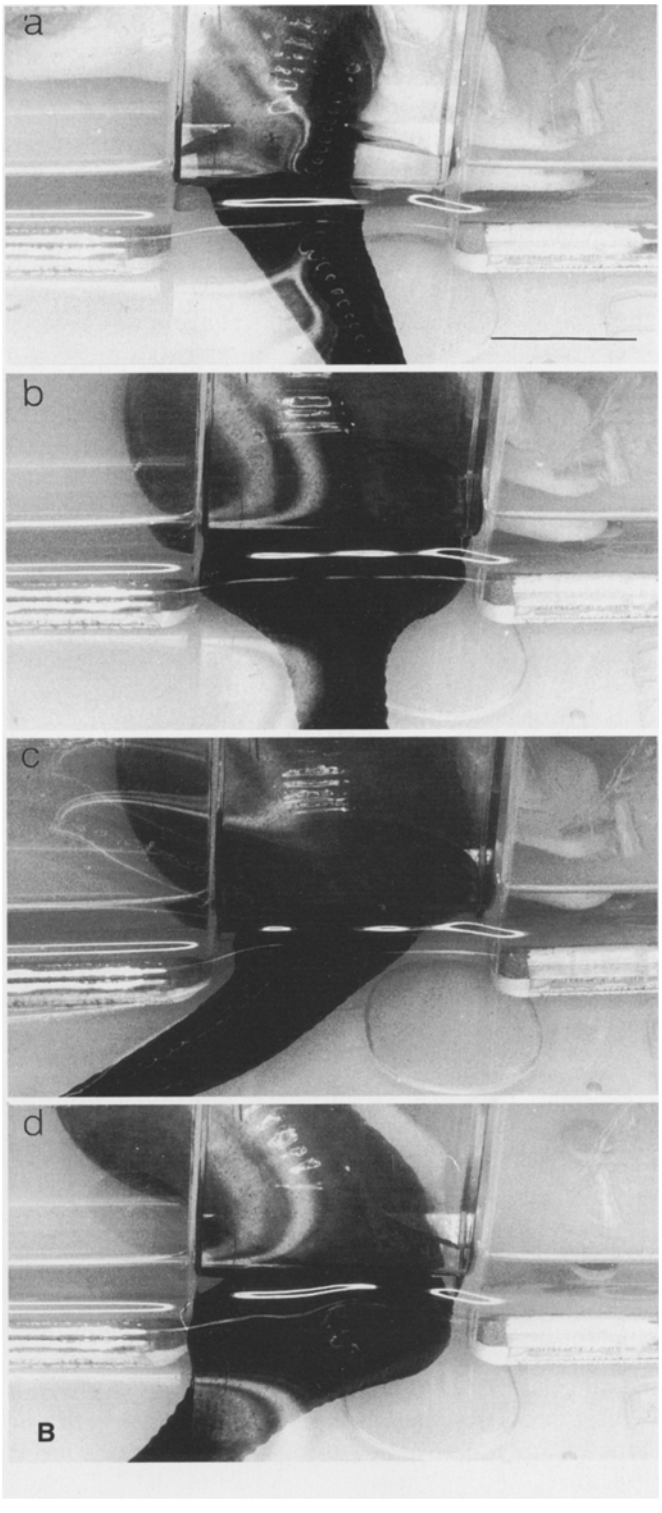
Response of T, P and N cells to increasing pressure applied to the skin

We used two probe sizes to measure the response of the mechanosensory cells to pressure on the skin. Initially the same 19×1 mm probe was used that formed the top of the aperture in the first experiments. This was successful only for T cells and a few P cell experiments. We were able to record T cell activity by suction electrodes applied to the surface of the ganglion, confirming intracellular recordings for these cells. Although we would have preferred to have used the large probe employed in the behavioural experiments for threshold measurements, the force and consequent movement of the ganglion with respect to the recording intracellular electrode required to activate N cells with this probe made threshold measurements for these cells unreliable, so for these, and most P cell threshold experiments, we used a probe with a much smaller contact area.

Any probe, pressed against the skin will exert a local pressure on the skin and its constituent cells in the area underneath the foot of the probe which will deform the skin and the nearby terminals of the mechanosensory cells. Larger applied pressures will deform the skin more than smaller pressures, although the exact relationship between pressure and skin distortion will be modified by the viscoeleastic properties of the skin (Fig. 6). A larger probe will deform more terminals of a single mechanoreceptor than a small one, especially since the primary terminals of the T, P and N cells are distributed over all five annuli of each segment. Thus probe size may influence threshold values, depending upon how receptor potentials are summed in the cell. However, the few threshold values that we obtained for P cells using the larger probe (foot area = 19 mm^2, Fig. 4) were of the same order of magnitude as those obtained using the small probe (foot area = $0.2 \times 10^{-6}\,m^2$, Table 1), so that we felt justified in using the small probe to obtain threshold values for P and N cells. The apparently large value for the pressure required to elicit a response from a P cell by Nicholls and Baylor (1968, pp 746) was not at threshold, but well above it, judging by the vigorous response of the P cell.

T cells responded to incremental pressure steps only at low pressures. As the pressure on the skin increased, the response from the T cells diminished and at the highest pressures disappeared altogether. T cells resumed firing as the pressure was subsequently reduced (Fig. 3).





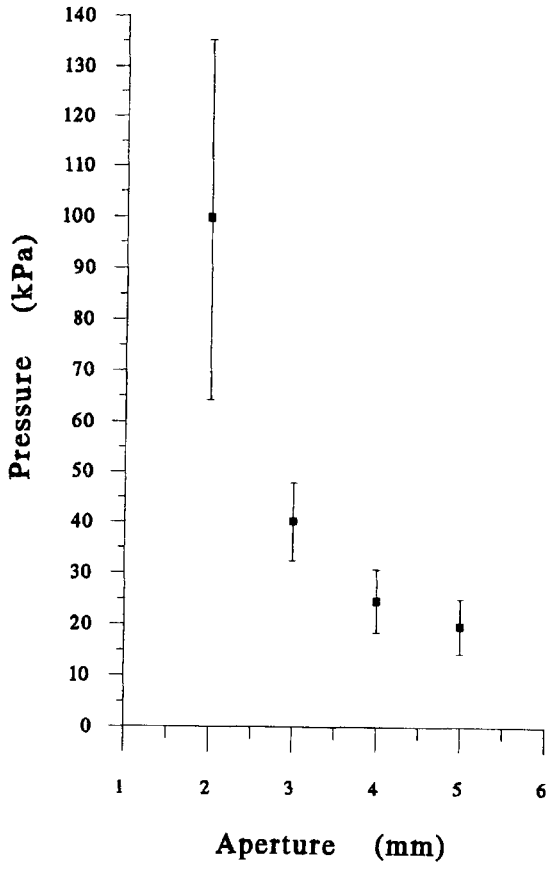


Fig. 2 The average maximum force exerted by 6 leeches weighing 2.6–3.7 g as they navigated apertures of different sizes. In each case the width of the aperture was 19 mm but the height was adjusted to the values on the graph. *Vertical bars* represent 1 SE

The response of P and N cells, unlike that of the T cells, was proportional to the pressure applied to the skin. P and N cells responded transiently to just-suprathreshold pressure increments and gave a more prolonged response as pressure increased beyond threshold (Figs. 4 and 5). A factor which may contribute to adaptation of these sensory cells is the marked relaxation which follows pressure increments, caused by stress-strain properties of the skin.

Since the ganglion was attached to the skin in these experiments, it was possible that the stress relaxation was caused by a neural reflex. We examined this possibility by measuring stress and strain engendered by

Fig. 1A, B Force generated as a 9.3 g leech squeezed through an aperture measuring 19 by 2 mm. The transducer measured the vertical force exerted by the dorsal surface of the leech. All traces in which the leech exerted a measurable force showed similar cyclical transients. The *vertical dotted lines* and letters *a–d* in **A** correspond to the *photographs* (**B**) which allowed the contact area between the leech and the force transducer to be measured. The *numbers* along the bottom give the calculated pressure exerted against the transducer for each photograph. In *b* the leech is moving towards the observer

Table 1 Threshold pressures for 5 P cells and 5 N cells

Cell	Number of positions	Threshold (kPa)
P1	4	162.4
P1	4	166.3
P2	7	131.4
P1	6	156.9
P2	5	137.0
N2	1	453.7
N2	2	545.8
N2	2	458.4
N1	4	613.7
N1	4	534.8

The second column indicates the number of different positions on the skin that were sampled in each preparation. Threshold is the average pressure that elicited action potentials. In each case a probe with a circular foot of 500 μm diameter was used

a probe indenting the skin when there was no ganglion present. Figure 6 shows that, as the skin is indented, pressure increases in a non-linear manner and declines rapidly after the probe stops moving into the skin. Pressure declines because the skin continues to move away from the tip of the probe (Fig. 6a) for some seconds. Mechanoreceptors which respond purely to movement of the skin may continue to fire for a short period after the probe has apparently stopped being driven into the skin, while cells that respond to pressure may cease to respond to the new position of the probe if pressure subsequently declines below the threshold. In both cases the duration and timing of the mechanoreceptor response will be conditioned by the stress-strain properties of the skin.

Velocity coding properties of T cells

The reduced response by T cells to pressure increments at larger pressures would be consistent with the idea that T cells respond to the velocity or amplitude of skin indentation rather than pressure, since both the

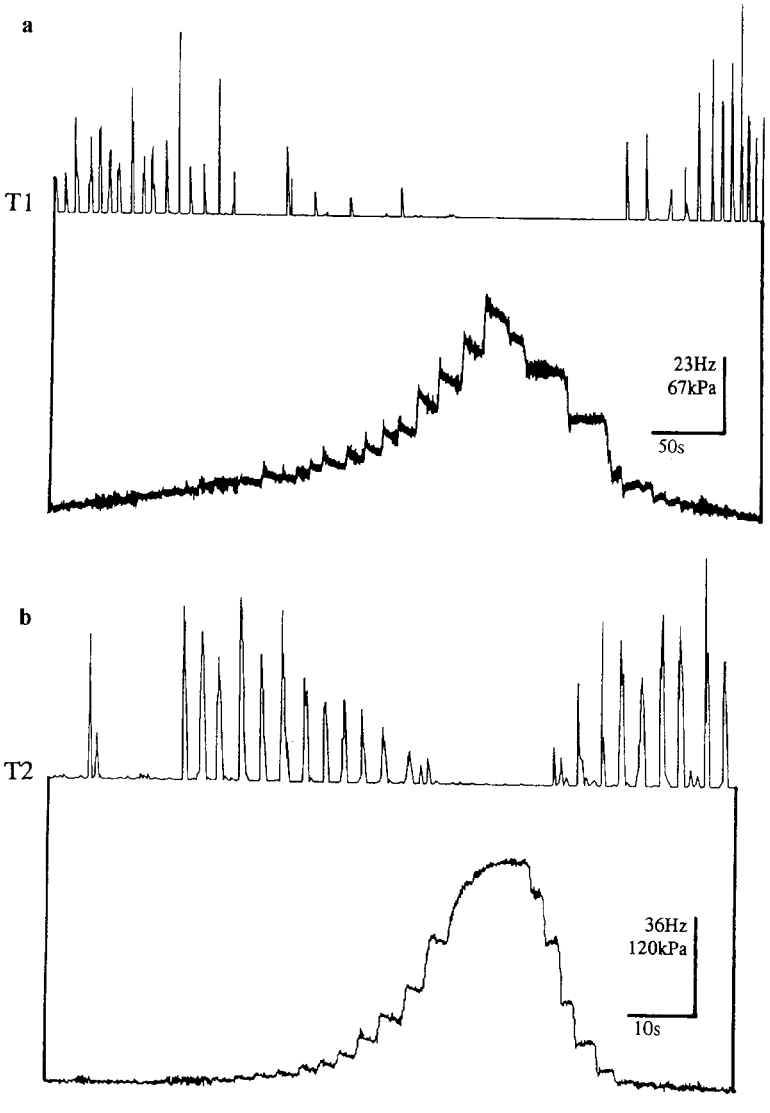
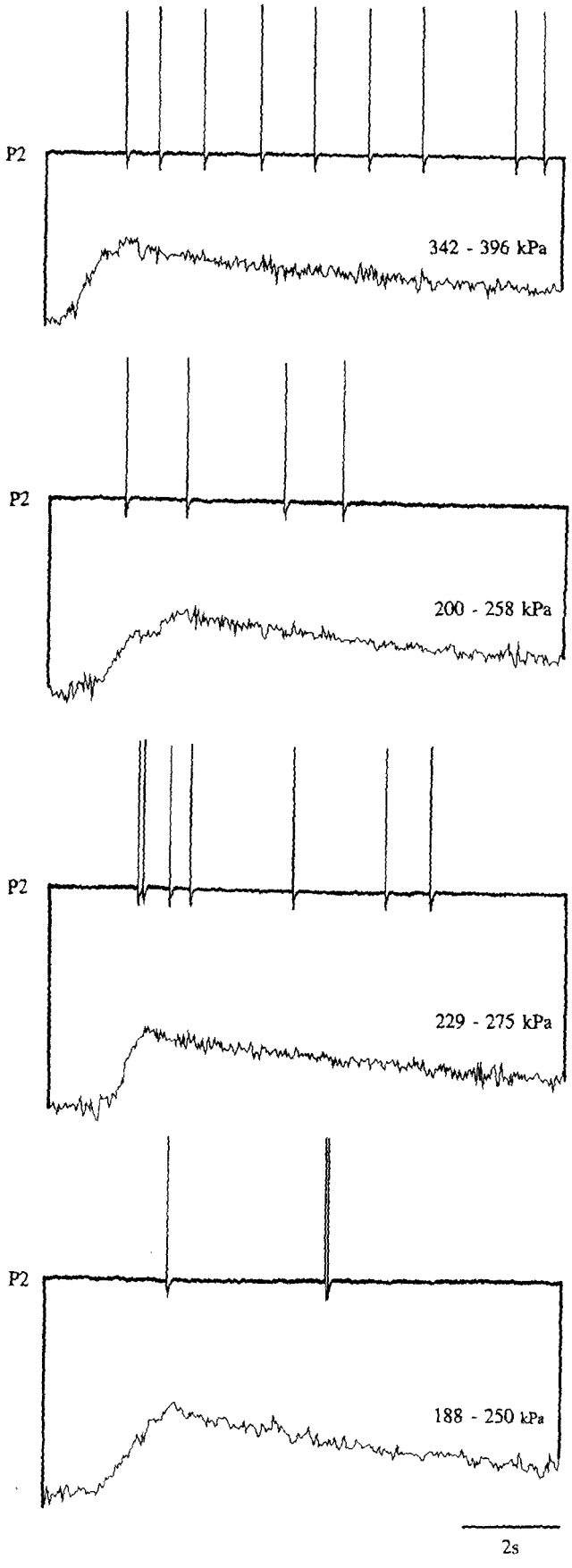


Fig. 3a, b Frequency at which a T cell fired (*upper trace*) in response to incremental pressures applied to the skin (*lower trace*) with a probe measuring 19 by 1 mm. In *a* the T cell record was obtained with an intracellular electrode. In *b* the response was recorded with a suction electrode applied to the ganglion sheath



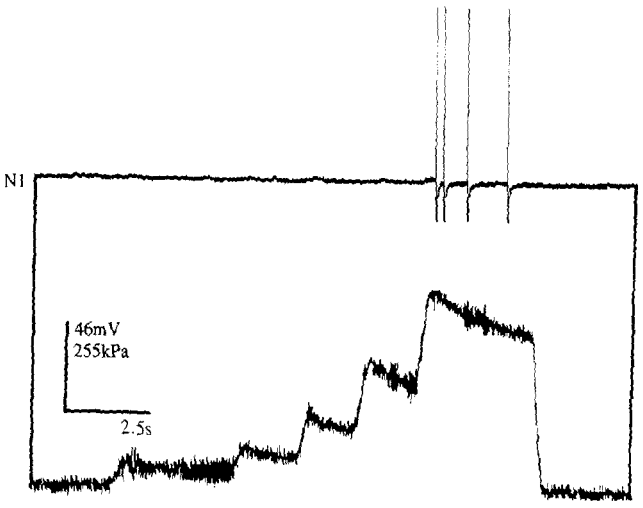


Fig. 5 Intracellular record from N1 in response to pressure increments which cross threshold. In this case the probe had a circular foot with a diameter of 500 μm

velocity at which the skin is indented and indentation amplitude will diminish as the pressure increases and the skin becomes progressively compressed. We measured the response of T cells to skin indentation over a wide range of velocities ranging from 10–9800 $\mu m\,s^{-1}$. T cells responded only to movement of the skin, which could be either indentation or relaxation (Fig. 7a). The frequency with which the cell fired tended to be higher at the beginning of the movement (Fig. 7b). When the response of T cells was examined over a wide range of velocities it became apparent that the frequency of action potentials in T cells was proportional to the log velocity, but this relationship is better described by two log functions rather than one (Fig. 8a). The velocity at which the transition to the second log function occurred varied with each preparation. Velocities as low as 10 $\mu m\,s^{-1}$ elicited spike frequencies above background.

Threshold values for P and N cells

We measured threshold pressures for P and N cells with a probe contact area of $0.2 \times 10^{-6}\,m^2$, thus reducing the force exerted on the whole preparation and consequently the movement artefact that prevented us obtaining repeatable values with the larger probe. Five P cells had thresholds which ranged from 131–166 kPa (Table 1). Threshold in these experiments was taken to

Fig. 4 Intracellular record of the response by P2 to incremental just supra-threshold pressure, applied to the skin with a 19 by 1 mm probe. The pressure at the beginning of the record and peak pressure is given in each instance. Pressure declined rapidly after each increment, accommodated by skin strain

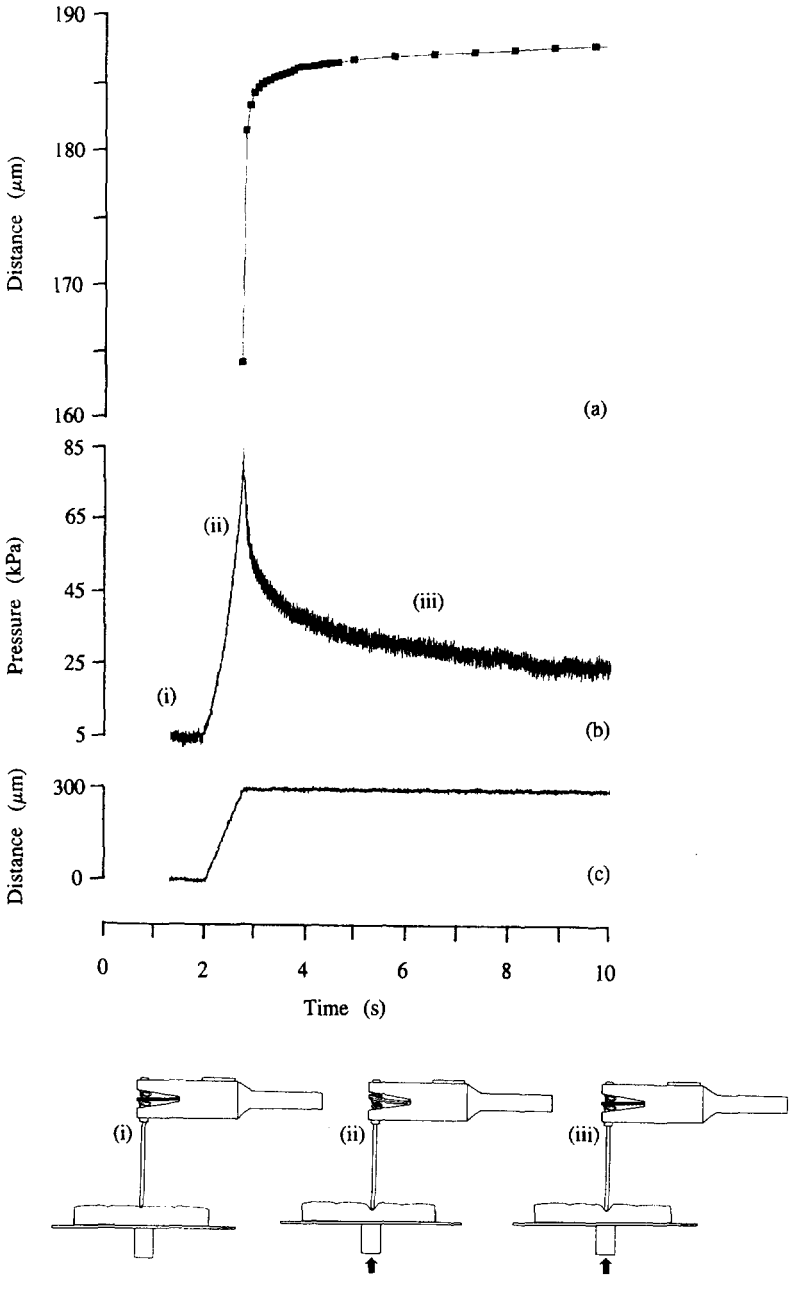


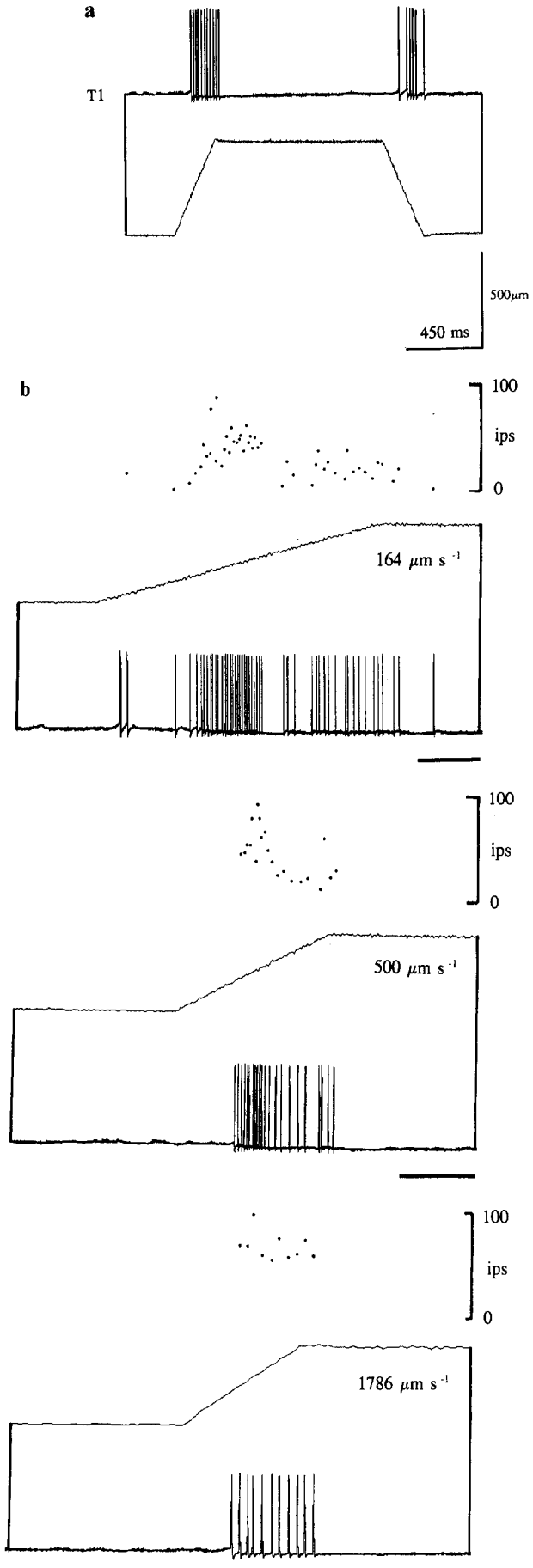
Fig. 6 Relationship between movement of the body wall (*c*) towards a probe that indents the surface of the skin and the resultant pressure (*b*) and movement of the skin (*a*) . In *a* only the movement of the skin under the probe, after the body wall has stopped moving, has been shown. *Diagrams* illustrate the relative position of the probe, and skin surface (*i*) before the body wall moves towards the probe (*ii*) as the probe begins to indent the skin and (*iii*) after the body wall has stopped moving but the probe continues to indent the skin as stress declines

be the occurrence of an action potential which coincided with an increase in pressure on the skin in a cell which had no spontaneous activity or whose spontaneous activity was 0.1 Hz or less. The threshold pressure for each P cell was determined at several positions close to the point on the skin which had proved to be most sensitive to indentation with a handheld probe. The threshold for five N cells, determined in the same way, ranged from 454–614 kPa (Table 1).

Discussion

These experiments have shown that T cells in the medicinal leech code for velocity of skin deformation. P and N cells respond when the pressure beneath the probe increased above threshold as shown earlier by Nicholls and Baylor (1968). Since maximum distortion of the cells underneath the probe will have been reached as pressure decreased to a minimum followed stress relaxation, is seems likely that P and N cells do respond to local pressure rather than strain since the frequency with which they discharged decreased after the point of maximum pressure rather than increasing. Electrical adaption may also contribute to the declining response of the cell following an increase in pressure. We did not attempt to separate the electrical and mechanical components of adaptation.

A comparison of the threshold for P cells and the pressure exerted by leeches moving through their



environment suggests that the P cells, at least over the body segments, are unlikely to be activated since their threshold is about 10 times higher than the pressure exerted against constrictions they can only just squeeze through.

If this is the case for P cells it must also hold true for N cells whose threshold pressure is 3.5 times higher than that of the P cells. At threshold both P and N cells fired single action potentials or only a few action potentials at low frequency. Debski and Friesen (1987) showed that 15 Hz was the minimum effective frequency that elicited fictive swimming in T, P or N cells, so the threshold pressure for activation of P and N cells is less than that required to elicit swimming though it may be sufficient to drive local reflexes (Lockery and Kristan 1990a).

The demonstration that T cells detect velocities of indentation as low as 10 $\mu m\,s^{-1}$ suggests that they are excited whenever leeches explore and move over objects and discontinuities in the substrate. Mammalian skin mechanoreceptors respond strongly to tangential movements over the skin (Darian-Smith and Oke 1980; Darian-Smith et al. 1980; Goodwin and Morley 1987) as do leech T cells (Nicholls and Baylor 1968). In primates both the velocity (Lamb 1983; Morley and Goodwin 1987) and the direction of movement of the stimulus (Gardner and Palmer 1989) can be coded by rapidly adapting afferents. Innervation density is important because there is a strong positive correlation between afferent density and direction sensitivity (Essick and Whitsel 1985; Essick et al. 1991; Gardner and Sklar 1994). In less densely innervated skin longer stimulus paths are needed to achieve the same level of discrimination. If, as in primates, directional discrimination is enhanced by smaller receptive fields, it is worth noting that the receptive fields for T cells are smaller in the anterior body segments of the leech, which is used to explore the mechanical environment, than in the body segments (Yau 1976), a direct parallel with the primate hand.

Velocity receptors are also present in the skin of other genera including the hagfish *Myxine glutinosa* (McVean 1989), embryonic *Xenopus* (Roberts 1980), the catfish *Ictalurus nebulosus* (Biedenbach 1973) and the lamprey *Petromyzon* (Mathews and Wickelgren 1978).

The frequency with which T cells fire in response to skin deformation can be described by two log functions of the general form $y = a + b \log x$, where y = frequency, x = velocity and b = a constant describing the

Fig. 7a Intracellular record from a T cell in response to a 500 μm indentation into and withdrawal from the skin by a probe travelling at a velocity of 2046 $\mu m\,s^{-1}$. The top *trace* shows the reponse of the cell, the *lower trace* represents probe position. **b** Intracellular record from a T cell to skin indentation at three different velocities. The depth of indentation was constant at 1 mm. The T cell tended to fire at a higher frequency at the beginning of indentation, as shown by the *top traces* representing instantaneous frequency. Scale bars in **b**, from top to bottom record, represent 500 ms, 500 ms and 200 ms

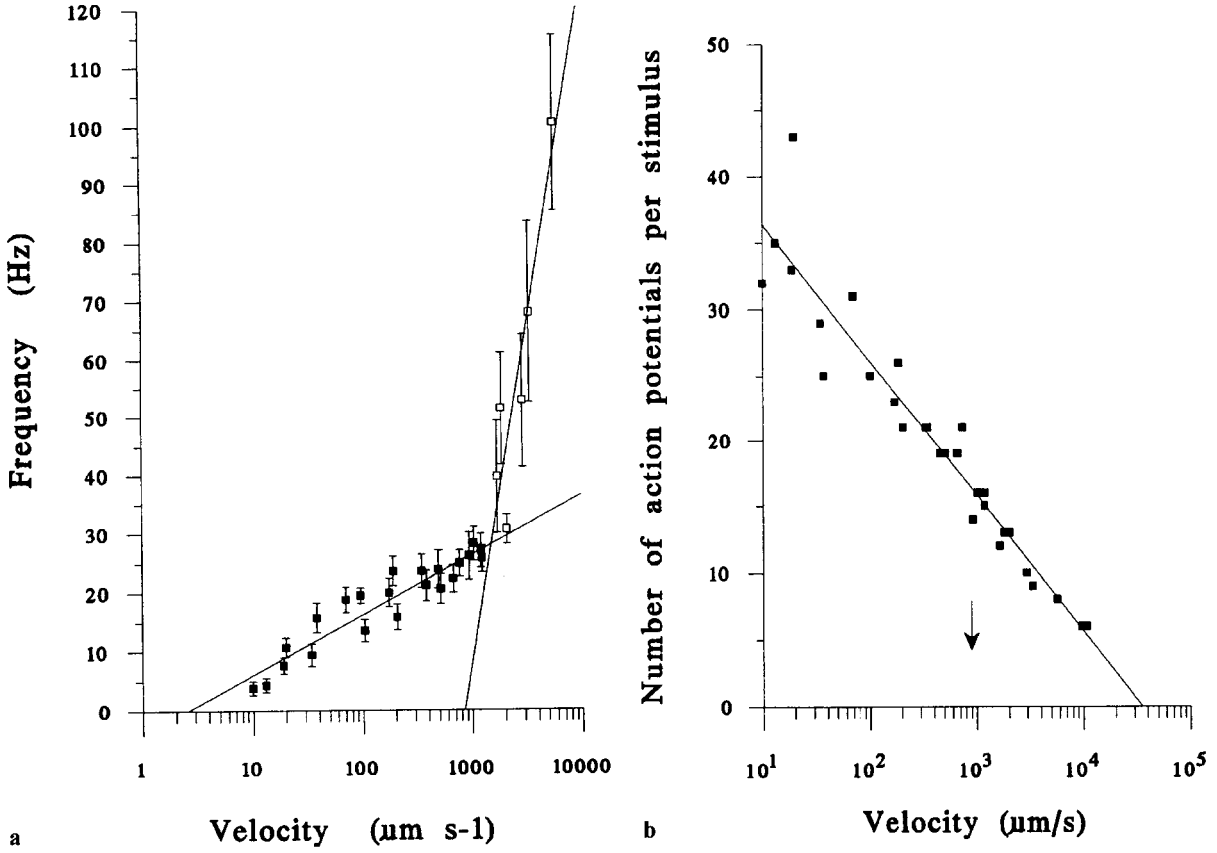


Fig. 8a The relationship between the frequency at which the T cell fires and velocity of skin indentation is best described by two log functions with different slope constants. The frequency was averaged over the period of indentation. The skin was indented at different velocities over a distance of 1 mm. **b** The number of action potentials per stimulus declines, as a log function, with the velocity of indentation. There is no break in the number of action potentials corresponding to the change of slope in Fig. 8

gain of the receptor. Within both the low and high range of velocities the gain of the receptor decreases with velocity, giving a wide dynamic range, but at the transition velocity (about 1000 µm s^{-1} in Fig. 8a) the gain of the receptor is enhanced. The average value for b at low velocities was 6.5 and above the transition point it was 68.1 ($n = 6$). The velocity at which this transition took place varied with each preparation. The relationship between velocity and frequency for the T cells is not best described by a power function (Uttal 1973) since double log plots fail to produce a straight line relationship.

Similar changes in gain have been observed in S and T non-spiking receptors in the crab *Carcinus maenas*. In these receptors the gain change also occurred at velocities in the region of 1000 µm s^{-1}. The constant b for these non-spiking receptors ranged between 1.7 and 12.0 for low velocities, while for the upper range of velocities its value increased to between 22.2 and 29.1 (Our calculations were done on data from Bush and Roberts 1971). Mechanoreceptors in the cement gland of embryonic *Xenopus laevis* (Roberts and Blight 1975) and rapid-transient mechanoreceptors in the skin of late *Xenopus* also exhibit similar changes in gain as velocity increases (Roberts 1980). As in *Carcinus* the transition in gain occurs in the region of 1000 µm s^{-1}.

What is the mechanism by which the gain of T cells is restored at higher velocities? One explanation might be that the probe initially covers just one receptor terminal in the skin and that as velocity of indentation increases the visco-elastic properties of the skin spread the area of indentation over a larger diameter circle until another receptor terminal is recruited. The distance between the terminals of T cells in the skin varies between 15 µm and 150 µm (Blackshaw 1981) a spacing equivalent to a density of 4444 and 44 terminals per mm^2 respectively. The probe used in our experiments had a contact area of 0.196 mm^2 so that it should have covered between 871 and 9 terminals. It is unlikely therefore that the increased gain can be attributed to one more terminal being recruited because that would not provide a large enough change in gain. An alternative explanation could be that terminals in an adjacent annulus are recruited at high velocities. These appear to join the main axon of the cell by distinct neurites (Blackshaw 1981). If each branch has a single spike initiating site, recruitment of an adjacent tree with similar gain properties and a new spike initiating site will produce

a change in slope of the log function, but again not enough to account for the average five fold increase which would require the addition of not one but five new spike initiating sites in a circle around the first.

The increased gain in the receptor could have been achieved by compressing, above the transition velocity, the same number of action potentials into shorter time intervals. Figure 8b however shows that this is not the explanation since the number of action potentials per stimulus continues to fall at velocities above 1000 $\mu m\,s^{-1}$. Similar gain changes in non-spiking receptors suggests that there may be a link between the way the visco-elastic properties of the cell change with velocity and the mechanism that opens ion channels in the receptor membrane. Because the gain of the receptor is low below the transition point, T cells function more like displacement receptors at low velocities and more like velocity receptors above the transition point. However even below the transition point the skin has to be moving at a finite, though low, velocity for the T cell to signal skin deformation.

These experiments suggest that T cells are important to the leech for interpreting its mechanical environment. Because they respond to the rate of skin indentation they will provide an instantaneous record of the change in shape of the skin as it is deformed by contact with external objects. It seems unlikely that the leech would be able to integrate this information to provide a second by second representation of the shape of its surface, especially since T cells respond to both increase and decrease of local skin strain. In contrast P cells which respond relatively tonically to sustained pressure, could provide a more integrated record of skin deformation, although the threshold pressure for P cells may only be passed occasionally. Proprioceptive information provides us with continuous information about body posture, while we use tactile information on a more localised time scale to interpret the properties of objects of interest. The leech may do the same.

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