J. exp. Biol. **116**, 121–139 (1985)
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THE EFFECTS OF BEHAVIOURALLY RELEVANT TEMPERATURES ON MECHANOSENSORY NEURONES OF THE GRASSHOPPER, *SCHISTOCERCA AMERICANA*

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Accepted 23 October 1984

SUMMARY

1. Grasshopper mechanosensory hair neurones respond to displacement of their associated hairs in a temperature sensitive manner: comparable increases in the number of spikes per stimulus result from increases in temperature with constant stimulus strengths and from increasing stimulus strengths at constant temperature. It is therefore not obvious that neurones in the CNS which receive inputs from mechanosensory hairs would be able to distinguish between these two parameters.

2. The temperatures which populations of mechanosensory hairs on the thorax, head and tarsus experienced were measured in freely moving animals. Animals in thermally heterogeneous environments spent 90% of the accounted time in locations where thoracic temperatures of 32–44 °C were maintained (the behaviourally 'preferred' range). Head temperatures covered a wider range, and tarsal temperatures the widest.

3. Different populations of mechanosensory hair neurones exhibited different sensitivities to temperature. Thoracic hair neurones were significantly more temperature sensitive than one of the two populations of head hairs studied, and tarsal hairs exhibited a pronounced temperature compensation in the behaviourally 'preferred' range. Wind sensitive head hairs, however, showed exceptionally high temperature sensitivities.

4. There is a negative correlation between the temperature sensitivity of a population of mechanosensory hair neurones and the temperature variability to which those neurones are normally exposed. Implications of this correlation for the central interpretation of mechanosensory input are considered.

INTRODUCTION

Small terrestrial ectotherms like insects can be frequently exposed to microclimates which differ greatly in their thermal characteristics (Parry, 1951; Willmer, 1982). Having a small heat capacity, an insect's body will respond rapidly to such environmental fluctuations. Variations in body temperature can affect the performance of the

Key words: Grasshopper, mechanosensory neurones, temperature, temperature compensation.

nervous system, as shown by several recent studies of the temperature sensitivities of individual insect neurones (Heitler, Goodman & Fraser-Rowell, 1977; Abrams & Pearson, 1982; Abrams, 1982; French & Kuster, 1982). Although the relationship between neuronal responses and temperature may be complex for neurones in the central nervous system (Heitler *et al.* 1977; Abrams & Pearson, 1982), the neurones associated with mechanosensory hairs exhibit an overall increase in firing frequency and decrease in threshold to mechanical stimulation when temperature is increased (Thurm, 1963; Bernard, Gahery & Boistel, 1965; Smola, 1970; Abrams, 1982). The velocity and, to a lesser degree, the extent of a mechanosensory hair's deflection are also reflected in the firing frequency of its neurone (Runion & Usherwood, 1968). Thus, changes in either stimulus strength or temperature can similarly influence the response of a stimulated mechanosensory hair's neurone, leading to potentially ambiguous inputs to the central nervous system (CNS).

An animal could reduce the influence of temperature on its mechanosensory neurones through thermoregulation. Many insects regulate their body temperature, and elaborate thermoregulatory behaviour has been described for the locust *Schistocerca gregaria* (Fraenkel, 1930; Waloff, 1963). Steep thermal gradients due to different microclimates (Parry, 1951; Willmer, 1982) could, however, result in different parts of the animal's body encountering different temperatures at the same time, depending upon its orientation with respect to these microenvironments or to the wind. Thermal gradients within the body are therefore possible (Digby, 1955; Uvarov, 1977; Casey, 1981), and different parts of the body could be exposed to different ranges of temperature overall. Because thermal and mechanical changes have similar effects on mechanosensory neurones' responses, it is evident that such thermal heterogeneity within the body and over time might greatly complicate the interpretation of sensory input by central neurones.

The present investigation addressed this issue in two ways. First, the temperatures of different parts of grasshoppers' bodies were monitored continuously as the animals moved about freely within thermally heterogeneous environments in the laboratory. In this way, the temperatures to which mechanosensory hairs on these body parts would be exposed under more natural conditions could be assessed. Second, the temperature sensitivities of different mechanosensory hairs were determined by measuring the changes in the number of spikes fired for constant mechanical stimuli as temperature changed. The hairs used for the neurophysiological study came from populations located on the parts of the body for which temperature measurements were obtained. The temperature sensitivities of these populations of hairs could then be correlated with the actual temperatures and the temperature variabilities to which they were exposed in the freely moving animal.

MATERIALS AND METHODS

Behavioural experiments

Adult *Schistocerca americana* (Drury) ranging in weight from 1·7 g to 3·0 g, were obtained from a crowded laboratory culture. The animals were reared at 32 °C

with 60 W light bulbs provided during the day as additional localized heat sources. Animals were on a 16L: 8D light cycle. All behavioural experiments were performed during the afternoon on animals which had been fed the day before. They were anaesthetized with CO_2 and implanted with 40-gauge thermocouples both in the head (3 mm into the mandibular adductor muscles) and in the thorax (6 mm into the metathoracic musculature). In five animals, thermocouples were also implanted in the abdomen. The point at which the thermocouple penetrated the cuticle was covered with a drop of beeswax, both to hold the thermocouple in place and to seal the wound. The leads from the thermocouples were secured to the animal by a thread which was passed through the posterior portion of the pronotum at two points and tied around the leads. Waxing the leads and the thread together prevented the leads from slipping. Temperature recordings from each of the implanted thermocouples were begun 1 h after the animal was removed from the anaesthetic, and were made continuously for 2–4 h on a Leeds & Northrup multipoint recorder. Tarsal temperatures were not measured directly but were estimated from the substrate temperature at the locations occupied by the animals.

Animals were free to move about within an arena which had an area of about 2000 cm^2, and was bounded on two sides by low walls, one black and one white. A heat lamp was positioned 17 or 22 cm above the substrate, and the arena placed within a 10 °C or 33 °C environmental chamber or set in the laboratory at room temperature (20 °C). Three thermally heterogeneous environments were thus available. Temperatures within these environments were measured with model grasshoppers. Models were used because air or substrate temperatures can vary widely over short distances and do not account for the convective losses and radiative heat gains that would occur in a living animal. A model affords a closer approximation of environmental temperature as the animal would experience it (Parry, 1951; Bakken, 1976). The models were constructed from 1 cm diameter copper tubing which was painted yellow, implanted with thermocouples, and sealed at either end with corks. Two models were used: one which rested directly on the substrate, and one which was raised 4 mm above the substrate by wire legs which were insulated from the model's body, to simulate a standing or stilting animal. These models were placed at specific locations within the arena, to obtain a measure of the temperatures available to the animals and the steepness of the thermal gradients. Upon completion of some behavioural studies, the animal was killed with an injection of ethanol and placed in locations which it had occupied during the experiment. The temperature of the dead animal was compared to that of a living animal in the same locations, and, in some cases, to the models as well. These were in agreement for most, but not all locations. The widest discrepancies were found in the 10 °C environment. This environment, however, had the steepest thermal gradient (see Results, Fig. 2), so small differences in positioning or slight postural adjustments could strongly influence the temperatures measured in these cases. The ranges of temperatures available to the animals in the three environments as measured by the physical models were: 10–53 °C for the 10 °C environment, 20–53 °C for the 20 °C environment, and 33–74 °C for the 33 °C environment.

The animals were left undisturbed and their locations noted at random intervals. Any shifts in the animals' locations within the environments or even in their orientations at a given location resulted in changes in the temperatures of at least some body parts, and these were recorded by the multipoint recorder. Data were obtained for eight animals in the 10 °C environment, six animals in the 20 °C environment, and five animals in the 33 °C environment.

Neurophysiological experiments

Animals to be used for neurophysiological recordings were first anaesthetized with CO_2. Their wings were removed and the stumps sealed with low melting point wax. The wax was also used to restrain the animals in such a way that movement at the recording site was minimized. Parts of the body not used for recording were restrained only as much as was required to keep the recording site stable.

Mechanosensory hairs from populations at the following locations were studied (Fig. 1): (1) between the first two pulvilli on the metathoracic tarsi, (2) around the mesothoracic spiracle, (3) on the mesothoracic episternum, (4) on the gena, (5) in fields 1, 2 and 5 of the wind-sensitive head hairs (Weis-Fogh, 1949). These populations were chosen on the basis of their general locations and their stability over 1–2 h of stimulation and recording. Extracellular recordings were made from the cut end of the hair shaft with a blunt microelectrode filled with a solution of 1·8% polyvinylpyrrolidon in 490 mmol l^{-1} NaCl and 2 mmol l^{-1} $CaCl_2$ (Thurm & Wessel, 1979; Abrams, 1982). The recording electrode was placed over a hair so that it was not

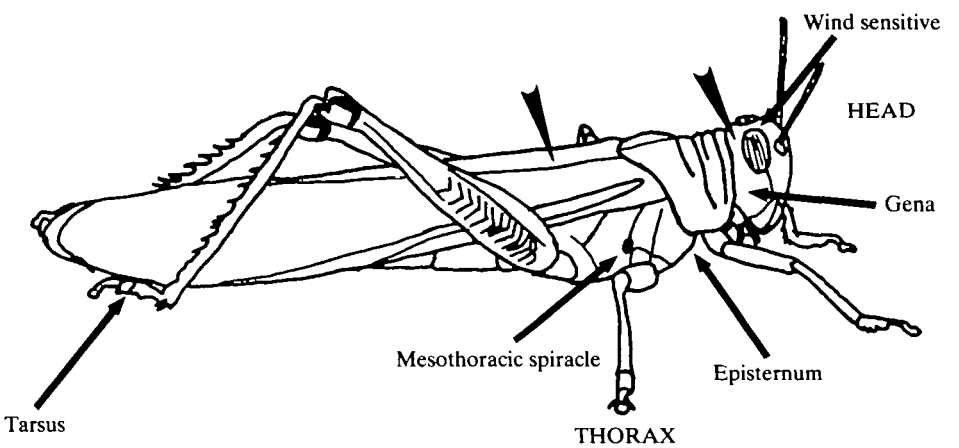


Fig. 1. Placement of thermocouples for behavioural experiments (arrowheads) and location of populations of mechanosensory hairs sampled in this study (arrows).

deflected unless the electrode was moved. None of the hairs which were used for recording produced spikes when in the undeflected (rest) position. A probe attached to the cone of a loudspeaker was used to deflect the electrode. The loudspeaker was driven by a trapezoidal signal, the rise time and amplitude of which could be varied (Abrams, 1982). By waxing the probe to the electrode holder, a constant stimulus could be repeated an indefinite number of times. For all hairs except the wind-sensitive head hairs, transient deflections 500 ms in duration were given at 10-s or 20-s intervals; wind-sensitive head hairs received 200-ms deflections with 4-s interstimulus intervals. The number of spikes elicited during each stimulus was counted using a window-discriminator and digital counter.

In most cases, the temperature of the cuticle around the recorded hair was varied by adjusting the intensity of a focused beam of light from a microscope lamp (Hegel & Casey, 1982). The light was inadequate for heating the foot, however, so this was accomplished by using a small heater made from high resistance wire supplied with an adjustable d.c. current. The wire was enclosed in glass capillary tubing, which was bent to fit beneath the foot.

Temperature in the immediate vicinity of a recorded hair was monitored with a 40-gauge thermocouple and a Bailey BAT-4 thermometer. The thermocouple was placed just below the surface of the cuticle, no farther than 1 mm away from the hair.

During an experiment, data were recorded on a Hewlett/Packard 7044A X-Y recorder. The number of spikes counted by the digital counter was routed through a D-to-A converter to the Y axis of the recorder. The temperature, measured by the thermometer, was displayed on the X axis. The pen of the plotter was activated following each response of the hair, thus producing an automatic plot (see Fig. 5) of response to a constant stimulus against the temperature of the hair. The plots were analysed by least squares regression.

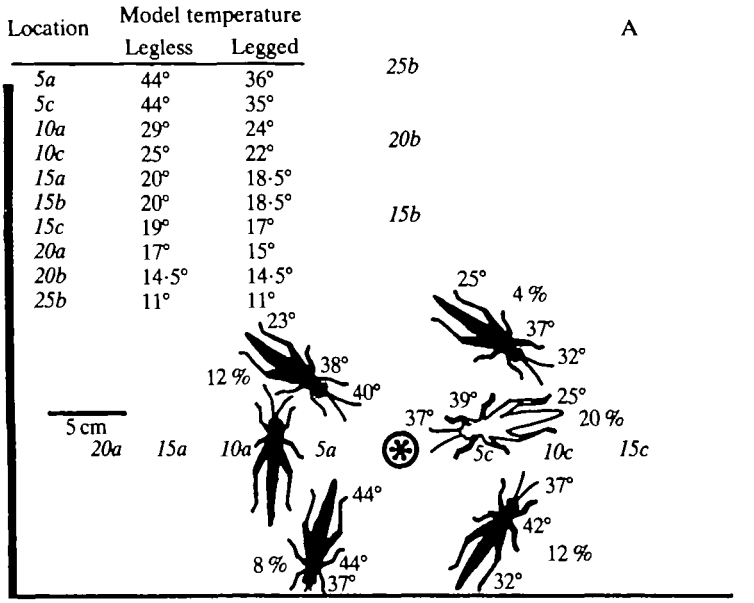
To obtain a measure of a hair's response to changing stimulus intensity at constant temperature, stimuli of the same duration and repetition rate as for the temperature experiments were used, but in this case the distance moved by the stimulus probe was varied. The distance which the recording electrode moved was measured directly with an ocular micrometer, and used as a measure of stimulus intensity. Stimuli of 24 different intensities were applied to each hair.

RESULTS

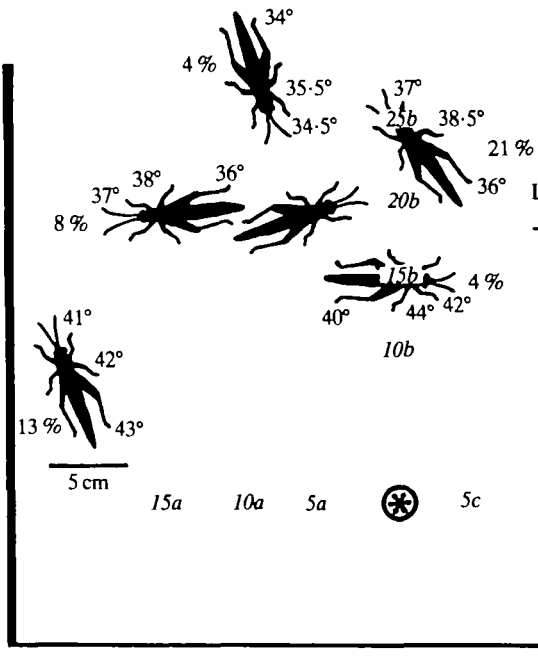
Behavioural studies

Animals in all three thermally heterogeneous laboratory environments displayed thermoregulatory behaviour by the locations they selected, by their orientations relative to the heat source, and by thermoregulatory postures (Fraenkel, 1930; Waloff, 1963).

Fig. 2 summarizes data collected for two individuals, one in the 10 °C environmental chamber, and one in the 33 °C chamber. The locations which the animals occupied and the relative amount of time spent at each are shown, in addition to the



Location	Model temperature	
	Legless	Legged
5a	44°	36°
5c	44°	35°
10a	29°	24°
10c	25°	22°
15a	20°	18·5°
15b	20°	18·5°
15c	19°	17°
20a	17°	15°
20b	14·5°	14·5°
25b	11°	11°



Location	Model temperature	
	Legless	Legged
5a	74°	57°
5c	63°	61°
10a	54°	51°
10b	47°	44°
10c	48°	46°
15a	46°	44°
15b	40°	39°
15c	43°	42·5°
20b	38°	37°
25b	34°	34°

Fig. 2

temperatures of head, thorax and tarsi. Note that the locations are different in the two cases; the animal in the 10 °C environmental chamber spent the majority of its time located considerably closer to the heat source than did the animal in the 33 °C chamber. Comparison of the environmental temperatures in the vicinity of the animals revealed that these were similar, both including the 35–40 °C range. Thus, both animals appeared to select locations within their environment that offered a similar range of temperatures. The actual thoracic temperatures of these two animals were likewise similar.

Closer examination of the actual temperatures measured for head, thorax and tarsi of the animals in Fig. 2, however, revealed that these could differ substantially at a given time. The animal in the 10 °C chamber showed much wider differences than did the animal in the 33 °C chamber. This may well have been due to differences in the thermal gradients of the two environments; measurements made using the model grasshoppers (see Methods) showed a much steeper thermal gradient within the area occupied by the animal in the 10 °C chamber than in the 33 °C chamber. Maximum temperature differences that were maintained between head and thorax for 3·5 min or longer ranged from 1 °C to 10 °C among the individuals studied. The average maximum difference for all animals was 3·6 °C. Between thorax and tarsus, maximum maintained differences ranged from 1 °C to 15 °C, with an average of 7·7 °C.

The direction and steepness of the thermal gradient measured within an animal's body usually corresponded to that of the environment, but exceptions did occur (Fig. 2A). In most of the locations this animal occupied, the thermal gradient within the body was in the direction that would be predicted from the environmental gradient. In one case, however, (open figure) the animal was orientated with its head nearest the heat source, yet the head was actually cooler than the thorax. Indeed, it was cooler here than in some locations that were considerably farther from the heat source. The animal had in this case extended its prothoracic legs, thereby raising its head well above the substrate. The temperature measured by the physical model held 4 mm above the substrate at this location corresponded to the temperature measured for the animal's head. Further analysis of the effects of orientation or thermoregulatory postures on body temperature was not attempted, as these were often subtle or only briefly maintained before the animal moved to an appropriate location in the thermal gradient.

Fig. 3 shows the relative time all animals in each environment spent with a given part of the body at a particular temperature. If data for thoracic temperatures in the

Fig. 2. Locations occupied by two individuals in thermal test arenas. The temperatures of each animal's head, thorax and tarsi are given alongside the illustrations of the animal's positions, as is the proportion of time spent at that position. Italicized numbers label specific environmental locations for which temperature was measured using the model animals. The temperatures measured at each of these locations are given in the table inset. ⊛, point of highest temperature. Walls in the environments are indicated by the axis-like lines, the heavy line representing the black wall, and the lighter line the white one. (A) Locations occupied by one animal in the 10 °C environmental chamber. Recording time, 187 min. Open figure: temperatures of head and thorax do not correspond to what would be expected from the environmental temperature gradient. Further discussion is in the text. (B) Locations occupied by an individual in the 33 °C environmental chamber. Recording time, 180 min. Each location was occupied for one continuous time period.

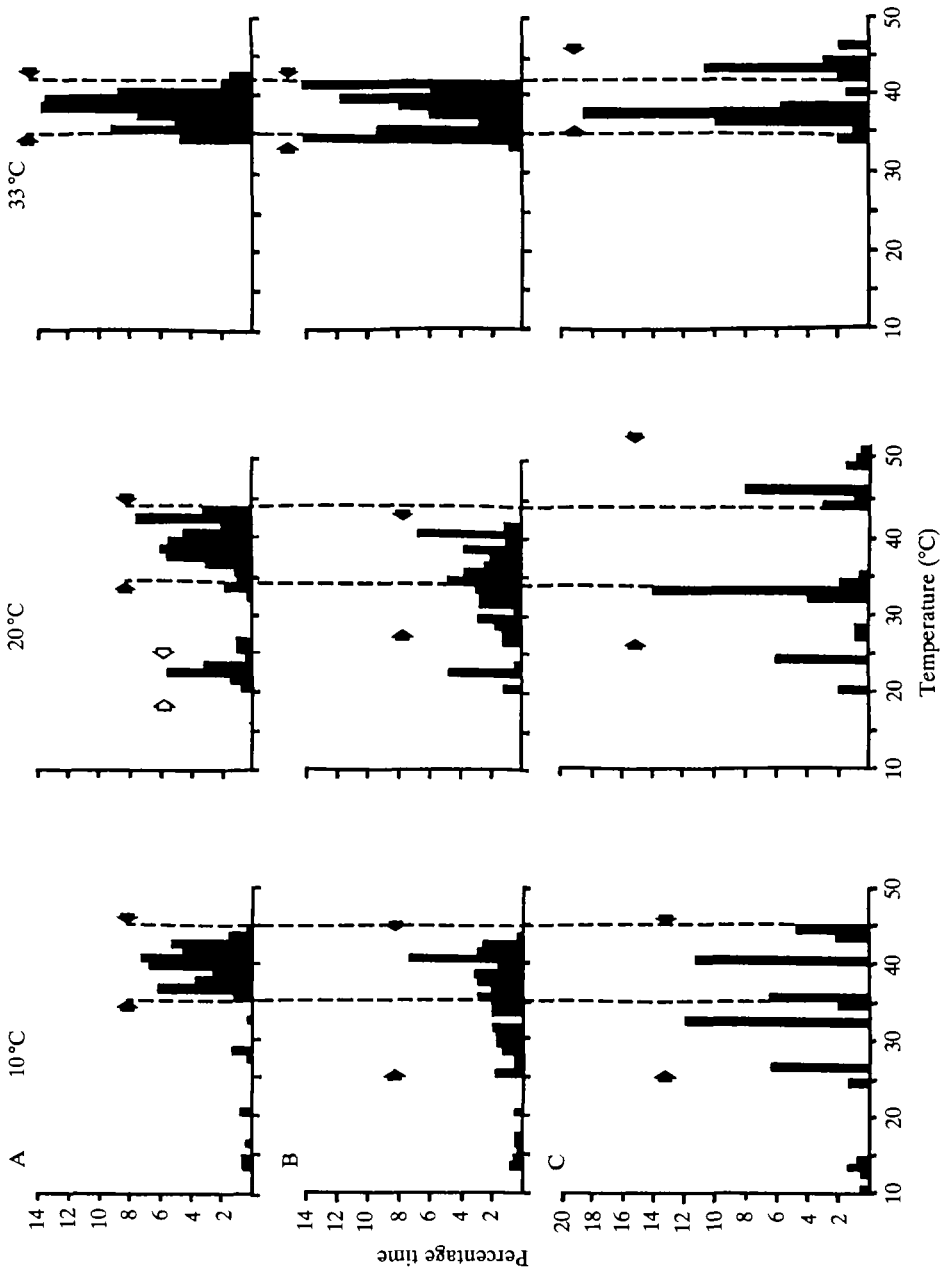


Fig. 3

three environments are combined, 90% of the combined data are found in the 32–44 °C range (Fig. 3A). The temperature ranges for the animal's heads are similar to those for the thoraces, but skewed toward relatively more time spent at lower temperatures (Fig. 3B). If these data are combined from the three environments, 90% of the resulting combination is found between 29 °C and 44 °C. The range of temperatures for the tarsi is considerably wider than for the head or thorax, extending to both cooler and warmer temperatures (Fig. 3C). Of the total accounted time in the three environments combined, 90% was spent in the 27–52 °C range.

Abdominal temperatures were recorded in five individuals. The temperature distributions for the abdomens of these animals were similar to those of their thoraces.

Neurophysiological studies

Fig. 4 illustrates the ambiguity that arises from comparable increases in the number of spikes fired per stimulus due to increases in either stimulus strength (Fig. 4A) or in temperature (Fig. 4B). Fig. 4C shows the number of spikes fired by a hair on the gena as a function of stimulus strength for three different temperatures. A 43% increase in the number of spikes fired per stimulus (Fig. 4C, asterisk) could be due to either a 9 °C change in temperature for the same stimulus, or a 10 μm increase in stimulus strength at the same temperature. It is also apparent from the slopes of the three curves in this figure that higher temperatures result in an increase in the sensitivity of the neurone to mechanical stimuli, as has been reported for other mechanoreceptors (Abrams, 1982; French & Kuster, 1982). Thus, if a mechanosensory neurone encodes the strength of its stimulus by its firing frequency and this information is important in behaviour, the nervous system must somehow compensate for the effects of temperature changes.

The effects of increasing and decreasing temperature on the number of spikes fired by different classes of hairs in response to a constant stimulus are shown in Fig. 5. The data for single hairs, shown in the left-hand column, were redrawn from those obtained directly from the preparation (see Materials and Methods). The plots on the right are composites of the regressions through the responses of all recorded hairs of each population. Table 1 summarizes the means of the slopes of these curves and shows that each of the four types of hairs exhibits a different sensitivity to temperature. The wind-sensitive head hairs (Fig. 5A) are considerably more sensitive

Fig. 3. Relative amounts of time which all animals in each of the three thermal environments spent with (A) thoraces, (B) heads and (C) tarsi at specific temperatures. Animals tended to remain in a given location for extended periods of time and temperatures which were maintained for less than 3·5 min are not included in this data. The figure therefore illustrates only the distribution of 'preferred' temperatures. Time is expressed as percentage of the total time spent by all animals in a given environment. The first set of thoracic, head and tarsal histograms is for animals in the 10 °C environment ($N = 8$). The pairs of arrows delimit temperatures which include 90% of the data. Dashed lines are drawn from the arrows in the thoracic histogram so that this range of temperatures can be compared with the ranges for 90% of the head and tarsal data. The second set of histograms is for animals in the 20 °C environment ($N = 6$). The peak of thoracic temperatures around 20 °C, marked by open arrows, is due to two individuals which spent extended periods of time at the ends of their thermocouple leads. However, 82% of the data lie between the solid arrows. Solid arrows mark 82% of the head and tarsal data as well. The third set of histograms is for animals in the 33 °C environment ($N = 5$). Arrows delimit 90% of the data.

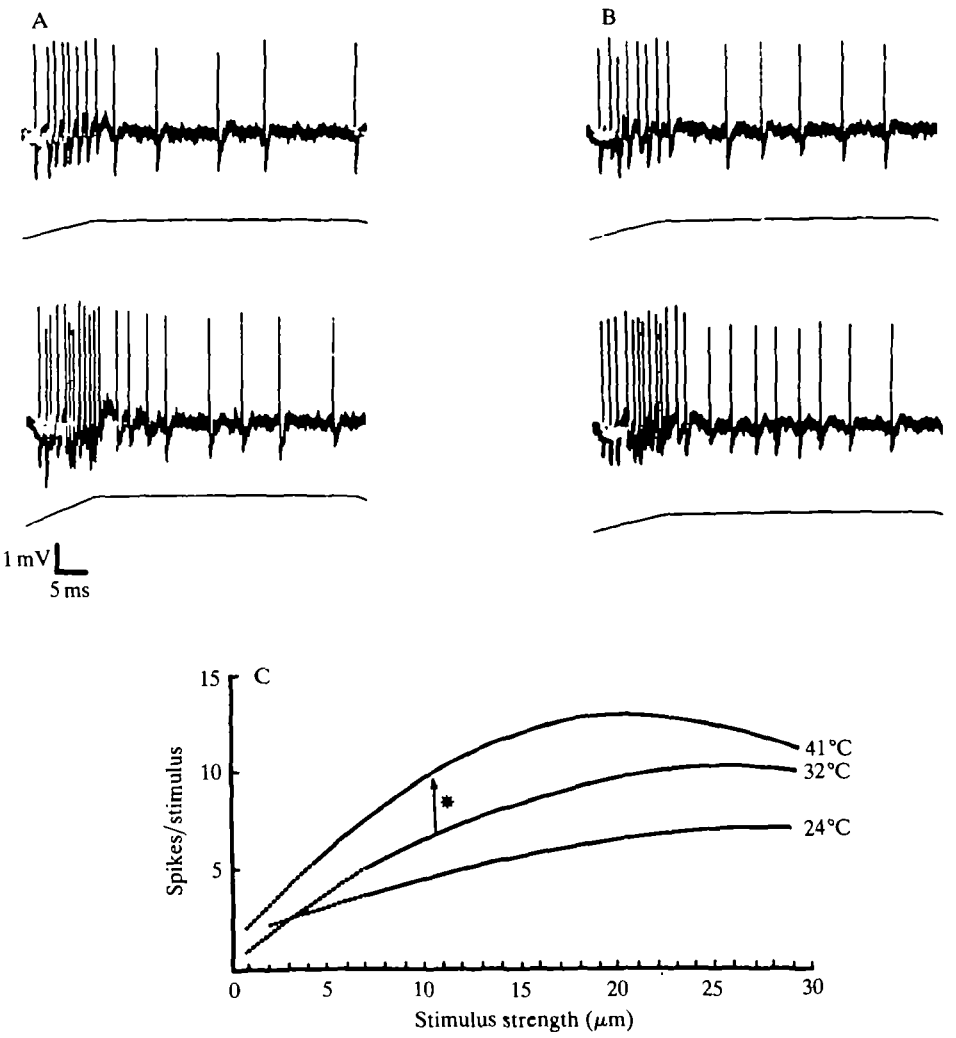


Fig. 4. Similarity of neuronal responses to increasing stimulus strength and to increasing temperature. (A) Effect of increasing the stimulus strength on the response of a thoracic hair to a single stimulus. The trapezoidal signal (rise time, 100 ms) which drove the stimulus probe is shown below the record of the hair's response. Upper record: 13 μm deflection. Lower record: 26 μm deflection. Temperature is constant (24 °C). (B) Effect of increasing temperature on the response of the same hair as in (A). Upper record: 24 °C. Lower record: 32 °C. Stimulus strength is constant (13 μm). (C) Responses of a hair on the gena to 24 different stimulus strengths at each of three temperatures; second order regressions taken from the data. Rise time of the stimulus was 100 ms and remained constant for all stimuli. Velocity as well as amplitude of deflection were therefore varied. For a typical genal hair 400 μm long, a 10 μm displacement of the stimulus probe represents about a 2° angular displacement at a velocity of 0·1 μm s^{-1}. Curves were considered significantly different where 95 % confidence bands on the curves did not overlap (solid lines). Where overlap occurred, curves are shown dashed. * indicates the 43 % increase in response discussed in text.

Fig. 5. Mechanosensory hairs' responses to a standard stimulus *vs* temperature. Plots of a representative hair from each population are given on the left; the regressions of all plots of hairs recorded from that population are on the right. No significant difference was found between data obtained by temperature increases and that obtained by temperature decreases; both are included in each plot. (A) Wind-sensitive head hairs. (B) Thoracic hairs. (C) Genal hairs. (D) Tarsal hairs. Regressions of A, B and C are first order; D is third order.

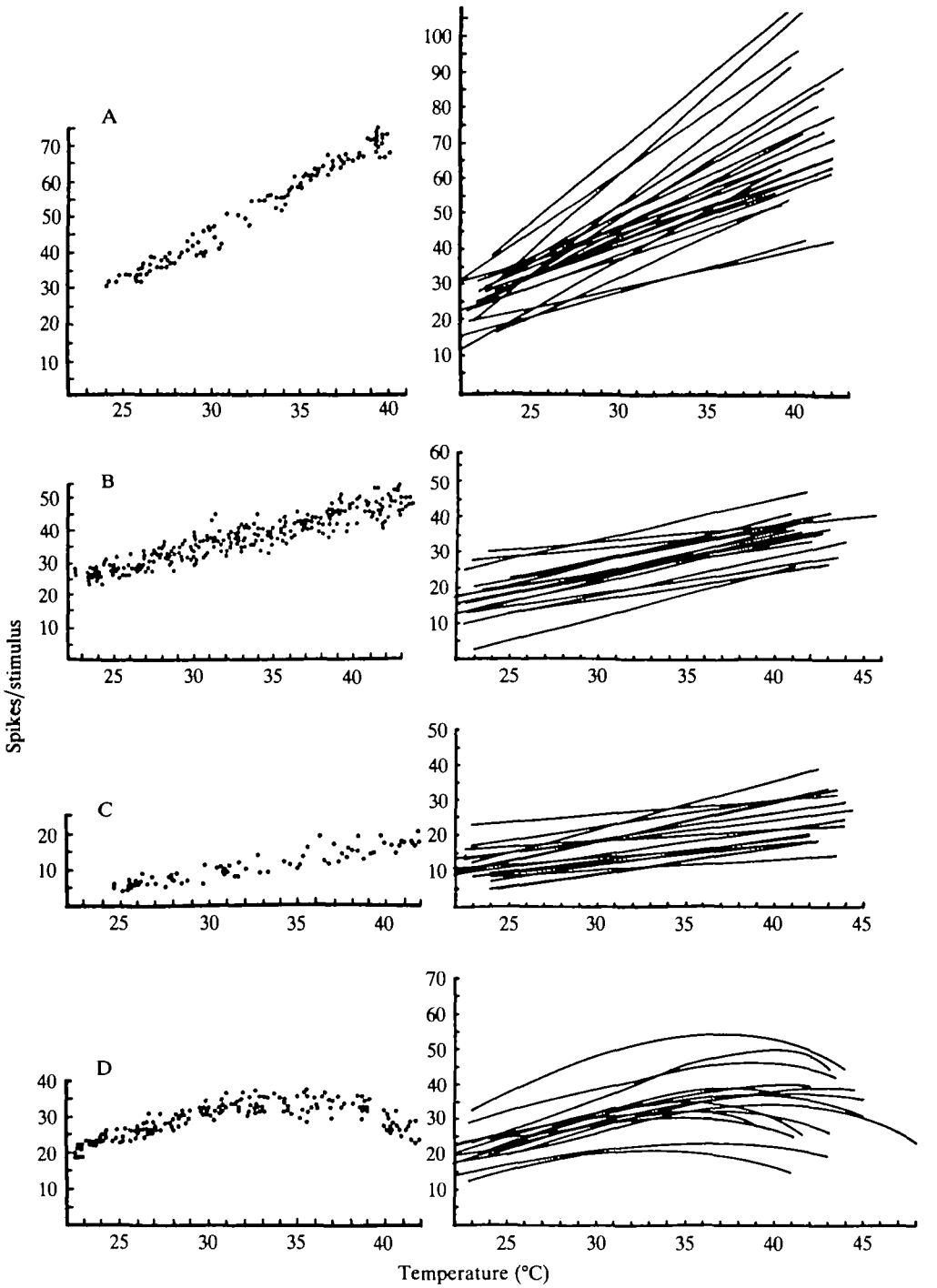


Fig. 5

to temperature than are the other hairs, with a mean slope that is twice as great as that of the next most sensitive population, the thoracic hairs (Fig. 5B). Hairs on the gena (Fig. 5C) are even less sensitive to temperature.

The response *vs* temperature curve of a tarsal hair (Fig. 5D, left) has a characteristically non-linear shape. The portion of the curve below 32 °C is linear like the

Table 1. *Mean slopes of response* vs *temperature curves for each hair population, expressed as mean ± 95 % confidence intervals (CI) of the mean*

Hair type	Head wind sensitive	Tarsal for T < 33 °C	Thoracic	Head genal	Tarsal for T > 33 °C
Mean slope ± 95 % CI	2·4 ± 0·4	1·28 ± 0·81	0·97 ± 0·12	0·66 ± 0·15	0·32 ± 0·13

Slopes are considered significantly different where the confidence intervals do not overlap. By this criterion, tarsal hairs below 33 °C and thoracic hairs are not significantly different. For temperatures ≥ 33 °C, the 'slopes' of the tarsal hair neurones were calculated from the difference between the maximum and minimum responses.

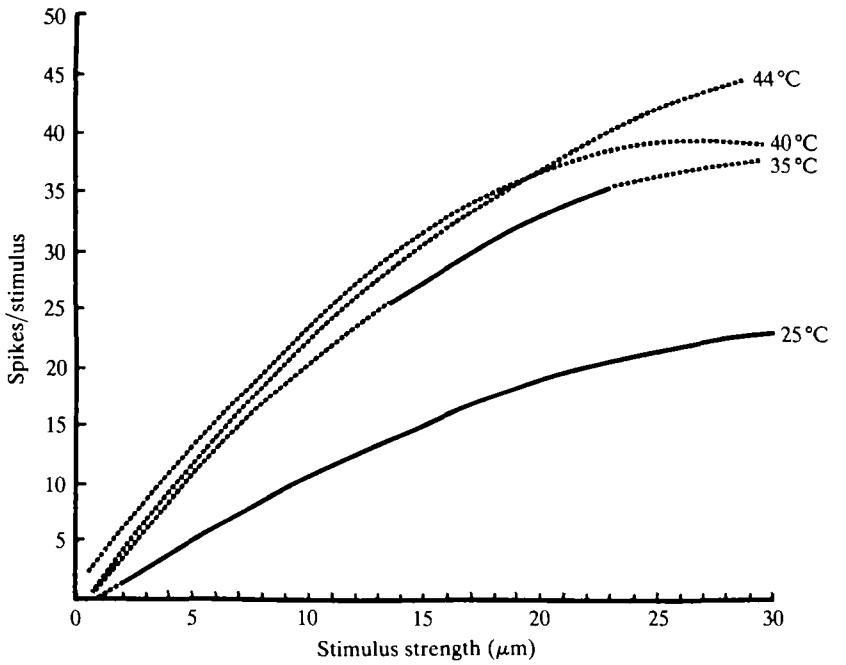


Fig. 6. Responses of a single tarsal hair to 24 different stimulus strengths at each of four different temperatures; second order regressions of the data. Rise time of the stimulus remained constant at 100 ms for all stimuli. Changes in stimulus strength therefore include changes in both velocity and total displacement. For a typical hair 400 μm long, a 15 μm displacement of the stimulus probe corresponds to approximately 2·8° of angular displacement, and a velocity of 0·15 μm ms^{-1}. Where the 95 % confidence bands on the regressions overlap, the regression curves are dashed. Curves are not considered to be significantly different where this overlap occurs.

curves for the other hair types, and the mean slope for the population of these hairs in this temperature range is similar to that of the thoracic hairs. For temperatures between 32 °C and 39 °C, however, the slope is close to zero, i.e. the response is almost perfectly temperature compensated, whereas above 39 °C the slope becomes negative. That the 32–39 °C region reflects temperature compensation and not saturation of the mechanosensory neurone is illustrated in Fig. 6. Here the relationship between the number of spikes fired by a tarsal hair and the strength of its stimulus is illustrated for four different temperatures. While increases in temperature from 35 °C do not result in significant changes in the number of spikes fired for a given stimulus strength, the number of spikes fired per stimulus will change if the stimulus strength is altered. Unlike the genal hair of Fig. 4C, this neurone's sensitivity to mechanical stimuli is about the same for all temperatures above 35 °C. Changes in spike number should, therefore, be interpreted simply as the results of changing stimulus strengths anywhere in this temperature range. All the tarsal hairs had similar response *vs* temperature curves, but the range of temperature compensation varied somewhat between individual hairs. To summarize the compensation of all the hairs studied, then, the temperatures at which perfect compensation occurred (where the regression through each response *vs* temperature plot had a slope of zero) for each hair are pooled in Fig. 7A. This figure shows that tarsal hairs are temperature-compensated in the 33–43 °C range.

As the population of tarsal hairs appears to be temperature compensated only over a specific range of temperatures, it is of interest to determine whether this range is one which would be especially significant to the animal. In Fig. 7, the histogram of temperature compensation (Fig. 7A) can be compared with a histogram derived from the data of Fig. 3C (Fig. 7B), which illustrates the proportion of time that animals free to choose their location within all three of the thermal environments spent with their tarsi at particular temperatures. This histogram shows that a majority (57 %) of the data lies within the 33–43 °C range. The tarsal hairs, then, are temperature compensated over the range of temperatures most frequently experienced by the tarsi. The range for physiological temperature compensation is therefore behaviourally relevant.

DISCUSSION

Behavioural results

In the behavioural studies, animals were free to move about within environments which offered a wide range of temperatures. These animals maintained thoracic temperatures in the 32–44 °C range, which is in agreement with temperatures measured for *Schistocerca gregaria* in the field (Waloff, 1963; Stower & Griffiths, 1966; Uvarov, 1977). Although animals adopted the thermoregulatory postures reported by Fraenkel (1930) and by Waloff (1963), they most frequently appeared to attain these body temperatures by their positions within the thermal environment. The temperatures of these positions, as measured with the model grasshoppers, are

within the range of environmental temperatures reported as 'preferred' or 'the zone of relative quiescence' in earlier laboratory studies (Chapman, 1965; Uvarov, 1966). There was no evidence in this study for physiological thermoregulation, as the temperatures of live animals and of dead animals or models were generally similar for a given location.

It was quite common for substantial *temperature differences* to be measured between the head, thorax, abdomen and tarsi. For an animal in its natural environment, even wider differences might be expected as these body parts are

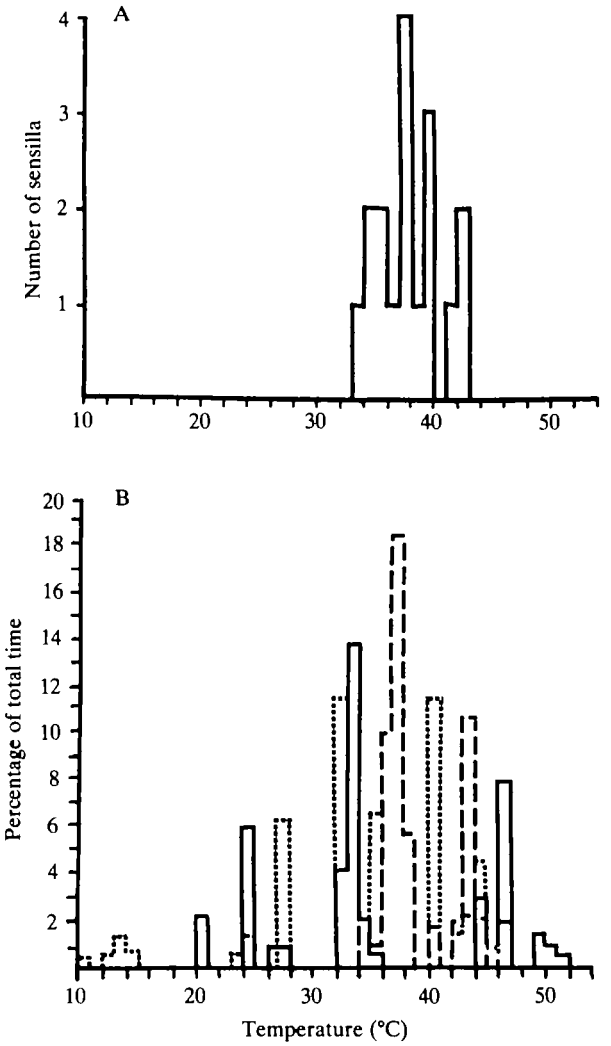


Fig. 7. (A) Temperatures at which slopes of the regressions through tarsal hairs' response *vs* temperature plots equal zero. (B) Relative amounts of time that tarsi of all animals in the behavioural study were at a given temperature. The data used here are the same as were used for Fig. 3C. · · · ·, 10 °C environment; ——, 20 °C environment; – – – –, 33 °C environment.

exposed to different substrates and variable degrees of shading, or are differentially exposed to wind. Furthermore, different body parts showed differing amounts of *temperature variability* with time (Fig. 3). Although thoracic temperatures reached as low as 13 °C, animals in the three thermal environments spent by far the most time (90 %) with thoracic temperatures in the 32–44 °C range. Head temperatures were less tightly clustered, extending to about 29 °C, though not above 44 °C, and tarsal temperatures were considerably more variable. A quantitative measure of the temperature variabilities of the head, thorax and tarsi will be discussed below.

Physiological results

As reported by Thurm (1963), Smola (1970), Abrams (1982) and T. W. Abrams & K. G. Pearson (in preparation), the mechanosensory neurones used in this study proved to be sensitive to temperature. Temperature-induced changes in neuronal response were of a similar magnitude to changes caused by different stimulus strengths.

The temperature sensitivity of an individual neurone can be expressed as the slope of the plot of its response to a standard stimulus *versus* temperature. The mean of these slopes can then be calculated for each population of mechanosensory hairs. A comparison of these means reveals that different populations of hairs have significantly different sensitivities to temperature (Table 1).

Wind-sensitive head hairs are the most temperature-sensitive of the hairs studied. They are, however, physiologically different from the other hairs in that they respond to displacement with very high firing frequencies and adapt only very slowly, maintaining high frequency discharges for many minutes (Camhi, 1969; Smola, 1970; Abrams, 1982). Similar responses have been reported for certain hairs on the cockroach leg (Pumphrey, 1936; Pringle, 1938; Wong & Pearson, 1976).

Wind-sensitive head hairs are important for the initiation and maintenance of flight (Weis-Fogh, 1949; Camhi, 1969) and have recently been shown to contribute to the central flight generator itself (Bacon & Möhl, 1983; Horsmann, Henzel & Wendler, 1983). The apparent lack of temperature compensation of the wind hairs could be due to compensation at other points in the wind hair/flight motor system. It is also possible that temperature compensation is unnecessary for this system, either because temperature is relatively constant in flight, or because the responses of the wind hairs, once they have reached a certain threshold value, are no longer relevant for the subsequent behaviour. It remains to be determined which, if any, of these possibilities is actually the case.

Populations of mechanosensory hairs on the gena of the head, in two locations on the thorax, and on the tarsi all show considerably lower firing frequencies and more phasic responses to mechanical stimuli than the wind-sensitive head hairs. In addition to these differences in firing pattern, the thoracic, genal and tarsal hairs are considerably less sensitive to temperature. The thoracic and genal hairs are, however, similar to the wind-sensitive head hairs in that their response *vs* temperature curves remain linear through the highest temperatures observed in the freely moving

animals. Although the functions of these particular sensilla have not been systematically investigated, it seems likely that they are tactile. Gentle stimulation of apparently similar sternal hairs has been found to elicit grooming responses (Fraser-Rowell, 1961). If the hairs are indeed tactile, then the nature of their stimuli, encoded by the firing frequencies of the sensory neurones, would presumably be important to preserve, and temperature compensation might be expected somewhere in the system.

The plots of the responses of tarsal hairs to standard stimuli *versus* temperature are clearly non-linear and are best fitted by a third order regression (Fig. 5D). For temperatures below about 33 °C, the mean slope for this population is similar to that of the thoracic hairs (the 95 % confidence intervals on the two means overlap), but above 33 °C these hairs show a strong temperature compensation. The range of temperatures over which the population exhibits perfect compensation (the fitted curves show a slope of zero) corresponds to the range of tarsal temperatures which animals in the behavioural studies maintained for a majority of the accounted time. At the highest temperatures in this behaviourally relevant range, the curves of individual hairs usually show a negative slope. At least some of the tarsal hairs studied here have been shown to respond to tarsal contact with the substrate and appear to be involved in both walking and postural adjustments. The firing frequencies of these hairs were observed to influence the activity of slow excitatory and inhibitory neurones which innervate the extensor tibiae muscle (Runion & Usherwood, 1968). Thus, temperature compensation in the receptors would be advantageous, resulting in consistent responses of the motoneurones, and hence the muscle, to given stimuli.

It is not clear what physiological mechanisms might result in different sensitivities to temperature among the different populations of mechanosensory hairs. Although at least part of the temperature sensitivity of insect mechanosensory neurones has been shown to be associated with the transduction of the mechanical stimulus to the generator potential (Abrams, 1982; French & Kuster, 1982), it is not clear what aspects of this transduction might vary between different hair types.

Because substantial temperature differences occur between different regions of a grasshopper's body (Fig. 2), populations of mechanosensory hairs on these regions must at least occasionally be differentially influenced by temperature. Since the effect of a change in the temperature of a mechanosensory hair can be comparable to that of a change in the strength of its stimulus (Fig. 4), it would be difficult for a neurone in the CNS which receives input from one or more mechanosensory hairs accurately to reflect real changes in sensory input, unless the effects of temperature were appropriately compensated. In principle, this could be accomplished by perfect compensation of all the receptors, but the data presented here show that this is not the case. An alternative mechanism would be to provide a degree of compensation that is related to the temperature variability actually experienced by different receptors. To determine whether this is the case, an attempt was made to correlate the temperature sensitivities of all but the wind-sensitive head hairs with the temperature variability of the region of the body where the hairs were located. The correlation is made only for temperatures above 33 °C, for three reasons. (a) This was the behaviourally preferred

range of temperatures; animals chose locations in their environment which offered temperatures above 33 °C, and by doing so, they limited the extent to which different body parts could differ in temperature. (b) The temperature sensitivity of the tarsal hairs showed different slopes below and above 33 °C. (c) This range of temperatures was available to all animals in all three thermal environments, so data from the three environments could be easily combined. The wind-sensitive head hairs were not included in this analysis because of the differences in their physiological properties (see above).

The temperature sensitivity of a population of hairs was taken as the mean slope of the population's response *vs* temperature curves. For tarsal hairs at temperatures above 33 °C, this was calculated from the difference between the maximum and minimum responses. Temperature variability was determined in the following way. Using minutes as units of quantity, the mean temperatures of the head, thorax and tarsi were determined from the behavioural data for each animal studied for temperatures greater than or equal to 33 °C. The variance about the mean was calculated and used as a measure of temperature variability.

When the temperature sensitivities of the hair populations on the thorax, gena and tarsus are plotted against the temperature variabilities of these parts of the body (Fig. 8), it becomes apparent that hair populations on parts of the body that are exposed to

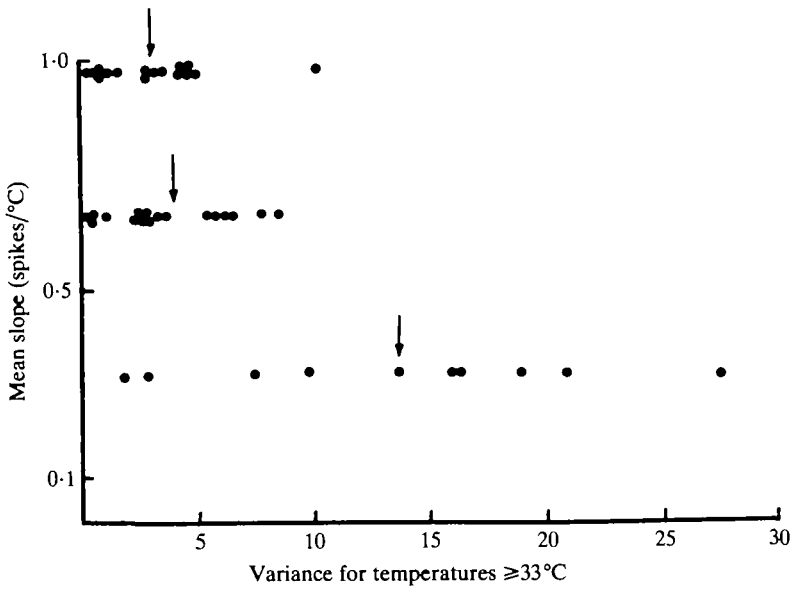


Fig. 8. Plot of temperature sensitivities of hair populations *vs* temperature variabilities of the parts of the body where each population is found. Temperature sensitivity is expressed as the mean of the slopes of the response *vs* temperature curves. Temperature variability is calculated as the variance about the mean temperature of head, thorax or tarsus for each animal studied. Arrows denote the mean values. There is a significant negative correlation between slope and variability (Spearman's rank correlation, $\alpha < 0{\cdot}01$). See text for further discussion.

greater temperature variability are less sensitive to temperature than are populations which are exposed to less variability. The correlation between temperature variability and neuronal temperature sensitivity is significant (Spearman's rank correlation, $\alpha < 0{\cdot}01$).

Thus, there are at least two mechanisms by which a grasshopper can minimize temperature-induced changes in the firing patterns of its mechanosensory hairs. One of these is behavioural: animals choose locations in their environment which offer a limited range of 'preferred' temperatures. The other is physiological: the mechanosensory hairs themselves are differentially sensitive to temperature, and the temperature sensitivity which the hairs of a given population exhibit is negatively correlated with the degree of temperature variability to which that population is regularly exposed. All hairs except the tarsal hairs do, however, retain a consistent temperature sensitivity over the full range of behaviourally relevant temperatures. Why all hairs are not temperature compensated like the tarsal hairs is not clear, and whether there are additional compensatory mechanisms which the nervous system might utilize for these hairs and for the highly temperature-sensitive, wind-sensitive head hairs remains to be determined.

I wish to thank Dr J. Palka for numerous critical readings of the manuscript and encouragement during the course of this investigation; Drs J. S. Edwards and D. J. Wigston for critical reading of the manuscript; and R. N. Miles for invaluable assistance with the data analysis. This research was partially supported by NIH training grant GM07108-09.

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