Response characteristics of cold cell on the antenna of *Locusta migratoria* L.

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**Summary.** The dendritic outer segment of the cell which is most likely the cold unit in the poreless coeloconic sensilla on *Locusta migratoria* antennae, has finger-like projections up to 1.5 μm long and 0.13 μm thick (Fig. 1). This unit responds to constant temperature, to slowly changing temperature and to step changes. Under stationary conditions impulse frequency attained 35 imp/s. Between 14 °C and 41 °C the higher frequencies were associated with the higher temperatures (Fig. 5). In this range the differential sensitivity is positive but not large: +0.8 (imp/s)/°C. Its resolving power for steady temperature is 4.7 °C.

Downward step changes produced by shifting between airstreams at different temperatures yield far higher frequencies (Figs. 2, 3). Step amplitudes were between −0.1 °C and −12 °C; the conditioning temperature from which the steps were initiated, was between 16 °C and 33 °C. Frequency peaked during the first 50 ms after stimulus onset (Fig. 2) and reached its highest values (310–340 imp/s) at initial temperatures above 30 °C and steps larger than −10 °C (Fig. 4). The mean differential sensitivity from 23 curves was −19 (imp/s)/°C and the resolving power 0.6 °C.

During slowly changing temperature the impulse frequency was governed by two parameters simultaneously: ambient temperature and its rate of change. Rates were between 0.001 °C/s or less, and 0.03 °C/s in either direction. Frequency was higher during slow cooling at a given temperature than during slow warming (Fig. 6). The average differential sensitivity to the rate of change was −210 (imp/s)/(°C/s). Further, the larger responses to cooling developed at lower ambient temperatures (differential sensitivity: −1.0 (imp/s)/°C). It is to be noted that this sign is negative, in contrast to the sign for differential sensitivity to constant temperature and also for the influence of initial temperature on the response to downward step changes.

**Introduction**

Although the number of arthropod cold receptors examined physiologically is still quite small and the precision and the completeness of the investigations differ greatly, considerable differences in response characteristics are emerging which suggest a relationship to biotope (see Table 1, Discussion). Presumably these differences reflect sensillum fine structure as well.

The three sensory cells of the poreless coeloconic sensilla on the antenna of *Locusta* are clearly thermo- and hygroreceptors (a cold cell, a moist-air cell and a dry-air cell). They are associated with a peg 4 μm long by 2 μm in diameter at the bottom of a pit about 8 μm deep and 15 μm at its widest. The opening varies between 5 and 8 μm. The moist and dry cells respond not only to humidity changes; the frequency of both tends to be higher at higher temperatures when relative humidity is held constant at zero (Waldow 1970). The cold cell responds to downward temperature steps with high frequency transients, but its stationary frequency also tends to be higher at higher constant temperatures. Nothing, however, is known of its ability to discriminate constant temperatures or step size, or even of its differential sensitivity to either of these parameters. Further, nothing is known of the range of the rates of temperature change capable of modulating the impulse frequency of this cell. For this reason the receptor was stimulated with slow, irregular, low-amplitude temperature oscillations, as was done with cold cells of *Periplaneta* (Loftus 1969) and the cave beetle *Speophyes* (Corbière-Tichane and Loftus 1983).

**Abbreviations:** b Slope of characteristic curve, differential sensitivity; F impulse frequency in imp/s; imp/s impulses/s; Pw partial pressure of water vapor in torr; r correlation coefficient; T temperature in °C; ΔT T-step; Δx resolving power in °C.
The sensilla housing the antennal cold cells of *Locusta* might be confused with other coeloconic sensilla on the same antenna, were it not for known differences in their structure (Altner and Loftus 1985). The type studied here is poreless. The dendritic outer segments of two of its sensory cells are unbranched and fit tightly into the sensillum; whereas the third is shorter and terminates below the socket. The dendritic outer segment of this cell branches into slender finger-like projections 1.5 μm long by 0.13 μm in diameter (Ameismeier 1985; Fig. 1). The other type has pores and its walls are double. Of the 2-4 sensory cells projecting up into the lumen, none is branched (Altner et al. 1981). These cells respond to food odors (Boeckh 1967; Kafka 1970) and in some cases one of them appears slightly sensitive to downward temperature steps (Altner et al. 1981).

The object of this paper is a detailed description of cold-receptor response characteristics in an ecologically and economically important subtropical orthopteran. In the background there is a further question of the extent to which the demands of cold cells in just one species. For the necessary comparison many representatives will be required from different biotopes. But that at least some of the material needed for the comparison might be provided in the case of *Locusta*, additional details characteristic of its dendritic end structures are also offered.

**Material and methods**

**Electrophysiology**

**Positioning and recording.** The adult *Locusta migratoria* used in these experiments were raised at 32 °C. Following their anesthesia with CO₂, an antenna was fastened with transparent tape along a narrow plexiglass ridge for unobstructed stimulation with airstreams at various temperatures and humidities. Impulses were recorded extracellularly with tungsten electrodes (tip diameter under 2 μm). One was inserted into the head; the other was driven along the peg into the floor of the pit. Recording was not begun until about 15 min after electrode insertion.

**Temperature.** Quantitative stimulation was provided at all times by one of three airstreams emerging at 2.4 m/s from nozzles 7 mm in diameter and 20 mm from the preparation. Two (A and B) had the same temperature (T) but different partial pressure of water vapor (Pₒ); two (A and C) had the same Pₒ but different T. While one played on the preparation, the others were either directed away from the antenna or deflected by gates (for details see Loftus and Corbière-Tichané 1981). Thermostatically regulated heat exchangers controlled airstream temperature. Pₒ of the streams was set at easily reproducible, pre-calibrated values (Loftus 1976). Temperature was measured within 0.03 °C by a small thermistor (Fenwall Electronics, BC 32 L 1) 2 mm downstream from the sensillum.

**Differential sensitivity (b)** was estimated by the slope of the regression approximating a stimulus-response relationship. In parabolic regressions, b is the mean of the first differentials of a given curve at the abscissa values actually used to stimulate the cell.

**Resolving power (Δx)** is the difference between two single stimuli that a single cell of average differential sensitivity needs in order to identify the larger of the two with a given high probability (e.g. 90%). The two stimuli can be a pair of constant temperatures or a pair of T-steps. The lower the value of Δx; the greater the ability to discriminate.

Δx was determined according to the equation:

\[ Δx = \frac{σ \sqrt{2}}{|b|} \phi_{\gamma}^{-1}, \]

in which b is the mean slope of all the regressions of a given type and σ, the standard deviation of the points about them. The symbol σ is used for the sample estimator here to avoid confusion with s, the symbol for seconds. \( σ = \sqrt{\sum (x^2/n-k)} \).

\( (n-k) \) indicates the degrees of freedom; n is the total number of points, I is the number of regressions, k is a factor designating the number of parameters needed to determine the regression, two for a linear and three for a parabolic. \( Δx \) is the sum of squared deviations from the regressions. \( \phi_{\gamma}^{-1} \) is the distribution function of a standardized, normally distributed, random variable. \( \phi_{\gamma}^{-1} \) is the inverse function of \( \phi_{\gamma} \). At a required probability of \( \gamma = 90\% \), \( \phi_{0.9} = 1.2816 \) (Diem and Lenter 1968, tables p.28).

**Stationary responses** were obtained from the impulse interval count to the nearest 0.1 interval from 4-s recording periods. The sensillum was exposed at each steady temperature for 10 min prior to recording. Steady temperatures ranged from 14 °C to 41 °C. Pₒ was maintained at 7.2 torr; relative humidity therefore varied between 60% at 14 °C and 12.5% at 41 °C. It was in this 27 °C-range that resolving power of the response for constant temperature was determined.

**Step changes** in T were provided by switching from a constant-temperature conditioning airstream (Tₒ) to another at a different temperature (T₂) for 1.9 s and then back to Tₒ for 5 min before the next step change. During this period Tₒ was altered. After a series of such steps, Tₛ was then set at another value and allowed to stabilize for 10 min before commencing a new series.

**Impulse frequencies (F)** of all series were determined by the number of impulse intervals during three different periods after stimulus onset, the moment at which T of the thermistor began to change. Since latency was not an object of this study, the first obvious narrowing of the interval between impulses after stimulus onset was taken as sufficient indication that a response to a downward T-step had begun. Thus the second impulse in the slightly narrowed interval was considered to be the first of the response. This was the first point in all three periods used to determine F. The final point was 50, 100, and 300 ms later. Since the final point of a period rarely coincided with an impulse, F in each case was determined by the number of entire impulse intervals within the period plus that fraction of an interval still included after the final impulse in the period. Thus F was the reciprocal of the number of impulse intervals to the nearest 0.1 interval for the measuring period.

The volume of the roughly cylindrical peg is only 12-14 μm³, but it sits in a pit. Consequently the T-transient within the temperature-sensitive structures during a step may be affected as much by T of the tissue underlying the pit walls as it is by Tₒ of the second airstream. In absence of precise data on the heat capacity and conductance of these structures,