Adaptation as a Mechanism for Gain Control in an Insect Thermoreceptor

Harald Tichy, Harald Fischer, and Ewald Gingl
Department of Neurobiology and Cognition Research, Faculty of Life Sciences, University of Vienna, Vienna, Austria

Submitted 29 April 2008; accepted in final form 4 August 2008

Tichy H, Fischer H, Gingl E. Adaptation as a mechanism for gain control in an insect thermoreceptor. J Neurophysiol 100: 2137–2144, 2008. First published August 6, 2008; doi:10.1152/jn.90514.2008. Adaptation controls the gain of the input-function of the cockroach’s cold cell during slowly oscillating changes in temperature. When the oscillation period is long, the cold cell improves its gain for the rate of temperature change at the expense of its ability to code instantaneous temperature. When the oscillation period is brief, however, the cold cell reduces this gain and improves its sensitivity for instantaneous temperature. This type of gain control has an important function. When the cockroach ventures from under cover and into moving air, the cold cell is confronted constantly with brief changes in temperature. To be of any use, a limit in the gain for the rate of change seems to be essential. Without such a limit, the cold cell will always indicate temperature change. The decrease in gain for the rate of change involves an increase in gain for instantaneous temperature. Therefore the animal receives precise information about the temperature at which the change occurs and can seek an area of different temperature. If the cockroach ventures back under cover, the rate of change will become slow. In this situation, a high gain improves the ability to signal slow temperature changes. The cockroach receives the early warning of slow fluctuations or even creeping changes in temperature. A comparison of the cold cell’s responses with the temperature measured inside of small, cylindrical model objects indicates that coding characteristic rather than passive thermal effects of the structures enclosing the cold cell are responsible for the observed behavior.

INTRODUCTION

Adaptation is a fundamental characteristic of information processing. It gives sensory systems the capability of adjusting the input-output gain to particular aspects of the stimulus even when the overall conditions of the sensory environment are changing. Such adjustments are observed as changes in the slope of the transfer function, corresponding to a multiplicative or divisive scaling, which is distinct from additive or subtractive shifting effects (Chance et al. 2002). Much attention has been focused on the trigger for changes in gain and the mechanism underlying gain control in the visual and auditory systems. In the temperature sensory system, however, the effect of adaptation on the input-output gain is less well understood, in part because of the difficulty in determining precisely the instantaneous values of temperature or even the rate of temperature changes at the receptive ending of the sensory cells.

Electrophysiologically, a series of experiments using rapid, step-like changes in temperature indicate two fast-acting adaptation mechanisms. One is sensitive to the magnitude of the step change with the consequence that the input-output functions tend to be steeper where the steps are smaller and to flatten as they become larger. The other is sensitive to the temperature from which the step change has been initiated. This means that the slope of the input-output functions is not same at all temperatures but steepest for one “best” temperature, flanked on both sides by functions of decreasing slopes. Examples are described for warm fibers of the facial pits of snakes (Hensel 1974, 1976) and the rat scrotum (Hellon et al. 1975), for warm cells of the tarsal organ of the wandering spider (Ehn and Tichy 1996), and also for cold fibers of the skin of rhesus monkeys (Darian-Smith et al. 1973), for cold cells on the antennae of the cockroach (Loftus 1968; Nishikawa et al. 1992), the stick insect (Tichy and Loftus 1987), and the locust (Ameismeier and Loftus 1988). The instantaneous values of temperature and its rate of change could not be determined at the receptive ending during rapid step-like temperature changes. Instead the temperature of the conditioning airstream and the difference in temperature between this airstream and a second airstream utilized to provide the steps were taken as parameters even though the rate of temperature change seemed to be the significant stimulus parameter.

In contrast to rapid step changes, where the temperature wave front is very steep, temperature values can be assigned from the airstream to the receptive ending during slow and continuous temperature changes, when the rate is low enough that the temperature of the receptive ending can be considered as locked to that of the air stream. During low rates of temperature change, the temperature of the air stream permits the determination of both the temperature of the receptive ending at each instant in time and the rate at which the temperature of the receptive ending is changing (Ehn and Tichy 1996; Gingl and Tichy 2001). This type of study, carried out on warm and cold cells of various insect and a spider species, revealed a dependence on both the rate of temperature change and the instantaneous temperature (Ameismeier and Loftus 1988; Corbière-Tichané and Loftus 1983; Ehn and Tichy 1996; Gingl et al. 2005; Loftus 1969; Loftus and Corbière-Tichané 1981). Therefore two parameters modulate the discharge rate of the thermoreceptors when temperature changes slowly.

In this study, we examined adaptation of the input-output gain to slow and continuous temperature changes in the cold cell on the antennae of the American cockroach (Fischer and Tichy 2002; Gingl and Tichy 2001; Loftus 1966, 1968, 1969; Nishikawa et al. 1992; Yokohari 1981; Zeiner and Tichy 2000). We used sinusoidal temperature changes because instantaneous temperature and the rate of change vary differently...
with the oscillation period. Hence it was possible to test the effect of different rates of change at the same instantaneous values and the effect of the same rate of change at different instantaneous temperatures. Specifically, we addressed the following two questions: does the cold cell change its sensitivity to instantaneous temperature or to the rate of temperature change when the period of oscillation varies over a wide range? Does adaptation perform a gain control function to improve the cold cell’s ability to encode changes in these parameters? We were additionally interested in possible mechanisms underlying the observed adaptation phenomena. Specifically, we investigated if the observed behavior could be accounted for completely by the physical state of the sensory structures or whether adaptation involves more complex changes in coding characteristics. We compared the time course of the discharge rate with the time course of the temperature monitored inside small, cylindrical model objects. We found that the phase difference is positive between the oscillating discharge rate and the oscillating air temperature, but negative between the oscillating model temperature and the oscillating air temperature. This indicates that the discharge rate is the outcome of active processing of temperature information rather than being defined in terms of the temperature input itself.

**Methods**

**Location and shape of thermoreceptive sensilla**

The whip-like antennae of the cockroach *Periplaneta americana* consist of 120–180 ring-shaped segments that grow thinner and longer with increasing distance from the head. The thermoreceptive sensilla are located on the distal half of the antennae, only on the ventral side near a segment’s most distal bristles. They are found often on alternating segments, ~20 per antenna and rarely more than one per segment. The sensillum is a small peg-shaped cuticular protuberance that projects at an angle of ~50° from the antennal surface and points distally to the antennal tip (Fig. 1). The peg is 6 μm long and 3 μm in diameter at its base, giving a volume of 42 μm$^3$. Using a cuticle of density 1.1*10$^{-9}$ mg/μm$^3$ (Shimozawa and Kanou 1984), the mass of the peg is 10$^{-7}$ mg.

**Preparation and recording**

The adult male cockroaches used in this study were obtained from a crowded colony maintained on a 12:12 dark/light cycle at temperatures between 22 and 25°C. Only animals with antennae exceeding 50 mm in length were used. Thus the flagellum extended ≥20 mm beyond the segments from which the recordings were made. Following anesthesia with CO$_2$, an animal was fixed dorsal-side-down on a closely fitting Perspex holder with the head and the antennae protruding. The head was immobilized in this position with a notched Perspex yoke slipped between the head and the thorax. Wings and legs were immobilized with strips of Parafilm wrapped around the holder. For unobstructed stimulation with airstreams at various temperatures, the antenna was fastened with dental cement (Harvard Cement) on the edge of a narrow Perspex ridge projecting laterally from the holder. Action potentials were recorded extracellularly with electrolytically sharpened tungsten electrodes. One electrode was inserted lengthwise into the tip of the antenna and the other at the base of the sensillum. The signals from the electrodes were amplified, band-pass-filtered (0.03–3 kHz) and displayed conventionally, passed through a CED 1401-micro (Cambridge Electronic Design, 12 bit, 300 kHz) interface connected to a PC for on-line recording. The data were stored on a hard disc and analyzed off-line using commercial software (Spike 2).

**Stimulation**

Continuous changes in temperature were applied by a single air stream merging at 2.5 m/s from a 7-mm nozzle. The air stream flow rate was controlled by passing it through a mass flow meter. The temperature was varied by thermostically subjecting a heat exchanger to slow temperature oscillations. Single oscillation periods took from 42 to 770 s. The partial pressure of water vapor was set at reproducible, precalibrated values (for details, see Tichy 2007). Rapid step-like temperature changes were produced by switching from one stream at steady temperature to another at lower steady temperature for 2 s and then back to the initial temperature. Air stream temperature was measured within ±0.03°C by a small uncoated bead thermistor (250 × 400 μm; Fenwall Electronics, BC 32 L1) 1 mm downstream from the sensillum.

**Rationales behind selecting the stimulus range**

The range of body temperatures at which an insect functions effectively is quite narrow, often little more than 4°C (May 1979). Electrophysiological studies on various insects, ticks, and spiders have shown that all thermoreceptors exhibit a static discharge at constant temperatures and a dynamic response to changes in temperature (Loftus 1978; Tichy and Gingl 2001). In the cold cell of the cockroach, *Periplaneta americana*, the static activity occurs at least in the range from 20 to 30°C with a maximum between 24 and 26°C. The dynamic activity is determined by the amplitude of cooling, with the greatest dynamic sensitivity corresponding to the maximum static sensitivity. Thus the cold cell’s response functions are characterized by a “best”
temperature (Fischer and Tichy 2002; Loftus 1966, 1968; Nishikawa et al. 1992). The present experiments were already performed within this “best temperature” range. The rates of temperature changes that were used to examine the discharge characteristics under oscillating stimulus conditions were similar to previous studies of the cold cell of the cockroach (Gingl and Tichy 2001; Loftus 1969), the cold cell of the locust and the warm cell of the tick (Gingl and Tichy 2001), the cold and warm cells of mosquitoes (Gingl et al. 2005) or the warm cell of the wandering spider (Ehn and Tichy 1996). All these thermoreceptors displayed interrupted response patterns when exposed to temperature oscillations between 1 and 0.1 Hz (Ehn and Tichy 1996; Gingl and Tichy 2001; Gingl et al., 2005; Loftus 1969); this complicated the quantitative description of the discharge rates. Therefore oscillation periods <0.02 Hz were not tested in the present study. Five different sine waves were selected, with periods between 42 s and 12 min (oscillation frequencies between 0.02 and 0.001 Hz). The separation between the sine waves was large enough for a tendency to manifest itself in the course of the oscillations’ periods, yet small enough to render very low the probability of a significant but unobserved bump or dip in the general course of the function. The lower limit was 0.001 Hz to finish the whole set of five sine waves within a reasonable period of 30 min. With two repetitions, we arrived at a recording period of 1.5 h.

The American cockroach is distributed throughout the temperate, tropical, and subtropical regions of the world. Although very adaptive, this insect prefers temperatures between 25 and 30°C (Baumholtz et al. 1997). The temperature in our rearing room was kept near 25°C. Provided that a water supply is constantly maintained, we had no indication that maintaining the temperature above ambient is of any advantage in rearing cockroaches. The present experiments were therefore conducted at laboratory temperatures between 22 and 25°C.

**Identification**

The cold cell occurs in the same sensillum with two hygroreceptive sensory cells. Most recordings (72%, n = 47) revealed the activity of all three sensory cells, but in some recordings (28%, n = 18), only two were detected. The cold cell was identified by its increase in impulse frequency to a drop in temperature, which was produced by shifting between two streams of dry air, the first at higher temperature and the second at lower temperature (Tichy 2007). A shift back to the initial air stream yielded an abrupt cessation of the activity. When the temperature change was repeated at moderate humidity, however,
both the cold cell and the hygroreceptors responded by changing their
discharge rates. Such reactions indicate receptors for relative humidity;
because relative humidity is defined as the ratio of the partial
pressure of water vapor to the saturation vapor pressure, it must
change when temperature changes and the vapor pressure remains
constant because the saturation vapor pressure changes with tempera-
ture.

**Impulse frequency**

Impulse frequency (imp/s) was determined by impulse count during
100 ms after the onset of rapid step-like stimulation. For responses to
slowly changing temperature, running averages of three consecutive
4-s periods were taken to measure frequency (Corbière-Tichané and
Loftus 1983). A 4-s period was used rather than the more common 1-s
period because the low rate of temperature change was reflected in a
slow change in the cells’ discharge rate.

**Model objects**

We made four model objects from Plexiglas. They were cylindrical
and weighed 4, 46, 115, or 440 mg. They all had the same surface-to-
volume ratio of 0.5. This ratio was important for a series of yet
unpublished experiments in which we tested the thermal effect of
infrared radiation. Here we describe data from a parallel study of the
thermal effect of convection. The air stream flowed along the lon-
gitudinal axis of the model objects or at an inclination of 60° with
respect to the longitudinal axis. The model temperature was measured
with a small bead thermistor (250 x 400 μm; Fenwall Electronics, BC
32 L1) positioned inside a central channel and fixed with Epoxy glue.

**Transmission factor**

The efficiency of the model objects in transmitting heat was
determined by the ratio of air temperature to object temperature.
Value 1 indicates that the model object attained air temperature. All
determined by the ratio of air temperature to object temperature.

**RESULTS**

**Cold cell responses**

To determine the gain for the instantaneous temperature and
the rate of temperature change, we exposed each of 45 cold
cells to five series of temperature oscillations with periods
between 42 and 770 s. In each series, a temperature range of
roughly 3.5°C between 18 and 24°C was covered and the rate of
change lay between –0.2 and +0.2°C/s. Figure 2 shows the
results of such an experiment. The top trace in each panel
represents the time course of the temperature oscillations with
periods of 42, 88, 200, 385, and 770 s, and the middle trace the
corresponding oscillations in impulse frequency. In general,
impulse frequency tended to be higher at the lower instantaneous
temperature values and lower at the higher instantaneous
values. The frequency values may be interpreted as the respon-
se to the instantaneous temperature. However, the oscill-
lations in impulse frequencies and instantaneous temperature
were not in step. The frequency curves led the temperature
curves. The phase difference was +5 s for an oscillation period
of 42 s, and +35 s for an oscillation period of 770 s. Thus the
oscillations in impulse frequency cannot be explained exclu-
sively by oscillations in the instantaneous temperature.

This impression is confirmed when comparing the time
course of impulse frequency with that of the rate of tempera-
ture change (Fig. 2, bottom traces in each panel). As the first
derivative of instantaneous temperature, the rate of change is
necessarily in advance of instantaneous temperature when the
temperature is oscillating. However, the oscillations in impulse
frequencies and the rate of temperature were not in step either.
The frequency values lag behind the rate of change, but in
general, the more negative the rate of change, the higher the
impulse frequency of the cold cell. The phase difference was
–10 s for an oscillation period of 42 s and –60 s for an
oscillation period of 770 s. Neither instantaneous temperature
nor the rate of change alone can adequately explain the impulse
frequency during slowly oscillating temperature changes.

To estimate the double dependence of the cold cell on
instantaneous temperature and its rate of change, the impulse
frequencies for the different oscillation periods were plotted in
Fig. 2 as a function of both parameters. The frequency curves
approached closed curves reminiscent of Lissajous figures in
which two oscillating magnitudes are plotted, one as a function
of the other. The figures indicate that the sequence of fre-

**Impulse frequency (imp/s)**

\[ a = 39.31 + \frac{83.07}{1 + (τ/55.25)^{1.8}} \]

**Gain for the rate of temperature change (imp/s°C)**

\[ b = 16.00 + \frac{300}{1 + (τ/2357)^{1.7}} \]

**Gain for instantaneous temperature change (imp/s°C)**

\[ c = 1.31 + \frac{3.01}{1 + (τ/62.52)^{1.7}} \]

**Error bars**

The error bars are SE.

**Figure 3.** A–C: variation of parameters of regression plane with the oscillation period. Regression planes calculated from impulse frequencies obtained from 45 cold cells with respect to corresponding values of instantaneous temperature (T, b slope) and the rate of temperature change (ΔT/Δt, c slope). A: the height of the regression plane (intersection with frequency axis, a) decreases exponentially with increasing oscillation period. B: the gain for instantaneous temperature (T, b slope) decreases exponentially with increasing oscillation period. The negative values for gain reflect the downward direction of the temperature change, yielding a rise in impulse frequency. Error bars are SE.
frequency values is too orderly to simply attribute phase differences during any oscillation period to random variation in the response.

Multiple regressions \( F = a + bT + c\Delta T/\Delta t \); where \( F \) is the impulse frequency and \( a \) the height of the regression plane were calculated to determine the simultaneous effect of instantaneous temperature \( (b \) slope) and the rate of change \( (c \) slope) on the response frequency during different oscillation periods (Fig. 2). In all 45 cells thus examined, the correlation coefficients \( (r > 0.99) \) show a strong linear relationship between impulse frequency, instantaneous temperature and the rate of temperature change. The square of the correlation value \( (r^2) \) indicates that an average of 98% of the variation in impulse frequency can be explained by the double regression. When the

![Diagram](image)

\[ Tm_{225} = 24.9 - 2.9\Delta Ta/\Delta t + 0.03 Ta \]
\[ Tm_{385} = 17.8 - 10.7\Delta Ta/\Delta t + 0.35 Ta \]
\[ Tm_{385} = 6.7 - 21.2\Delta Ta/\Delta t + 0.80 Ta \]

**FIG. 4.** A–C: time course of instantaneous temperature and the rate of temperature change of the air and a model object weighing 115 mg during slowly oscillating changes in air temperature. Oscillation periods (\( \tau \)) are indicated. During all oscillation periods, the oscillations \( (Tm) \) measured within the object lag behind the oscillations in air temperature \( (Ta) \); similarly, the oscillations in the rate of change in the model temperature \( (\Delta Tm/\Delta t) \) are behind those in the rate of change in air temperature \( (\Delta Ta/\Delta t) \).
correlation coefficient is reduced by its SD (±0.005), the percentage drops only to 97%.

The orderly relationships of impulse frequency to the instantaneous temperature and its rate of change during different oscillation periods provide an opportunity to determine the cold cell’s gain for each of these two parameters. In the example shown in Fig. 2, the gain for instantaneous temperature was –3.4 imp/s per °C for an oscillation period of 42 s (Fig. 2A) and –1.4 imp/s per °C for a period of 770 s (Fig. 2C); the gain for the rate of temperature change was –25.6 imp/s per °C/s for an oscillation period of 42 s (Fig. 2A) and –104.3 imp/s per °C/s for a period of 770 s (Fig. 2C, the negative values represent the downward direction of the temperature change, yielding a rise in the impulse frequency of the cold cell). The measurements show that during any oscillation period, impulse frequency can be influenced more by changing the rate of temperature change by 1°C/s than by changing instantaneous temperature by one additional degree. An increase of 1 imp/s during an oscillation period of 42 s can be elicited either by a –0.29°C decrease in instantaneous temperature (provided the rate of change is constant) or by a rate of change of –0.039°C/s. During an oscillation period of 770 s, it takes a decrease of –0.71°C in instantaneous temperature to increase impulse frequency by 1 imp/s (or a rate of change of –0.0095°C/s).

For all 45 cold cells, the values of the three parameters of the regression planes were pooled and plotted in Fig. 3 against the oscillation period. Exponential functions indicate that both the height of the regression plane (Fig. 3A) and the gain of the response for instantaneous temperature (Fig. 3C) decrease rapidly with increasing oscillation period. In contrast, the gain of the response for the rate of change increases rapidly when the oscillation period increases (Fig. 3B). Therefore the gain for the instantaneous temperature (Fig. 3B) is high when the oscillation period is brief and adapts when the oscillation period is longer. During adaptation of the gain for the instantaneous temperature, however, the gain for the rate of temperature change is improved (Fig. 3C). This improvement occurred during adaptation to instantaneous temperature. Adaptation is therefore a mechanism for gain control through which the cold cell increases its sensitivity to low rates of temperature change at the expense of sensitivity to the instantaneous temperature. These results indicate that the cold cell does not simply respond to the temperature changes as they occur at the receptive ending, but balances—from instant to instant—the response magnitude according to these temperature changes. To illustrate that such balance is an intrinsic property of the cold cell, we subjected small models to oscillating changes.

**Model objects**

The four cylindrical models weighing 4, 16, 115, and 440 mg were exposed to oscillating changes in air temperature. A sequence of three different oscillation periods of 60, 130, and 300 s was tested on each model object with rates between –0.2°C/s and +0.2°C/s. The temperature range covered was roughly 10°C between 19 and 25°C. Figure 4 is an example of the temperature change measured within the 115-mg model object. The top trace in each panel represent the time course of air temperature, the middle trace the time course of the model temperature, and the bottom trace the time course of the rate at which air temperature changed.

Two effects clearly emerged. One was that the temperature of the model object tended to oscillate at smaller amplitudes than air temperature and that the amplitude of the oscillations was not constant; it rose with increasing oscillation period (Fig. 4, middle). The dashed curves in Fig. 5A show that in all model objects the “transmission factor,” i.e., the ratio of air temperature to model temperature, increased exponentially with the duration of the oscillation period. As might be expected, the exponential functions tended to become steeper as the models became lighter.

The other effect was that the oscillations in the model temperature lagged considerably behind the oscillations in the

---

![Figure 5](https://www.jn.org/content/jn/100/5/1432/F5.large.jpg)

**Fig. 5.** A and B: variation of the transmission factor and the phase difference of the 4 model objects with the oscillation period. A: in the 4 models, the transmission factor increases with increasing oscillation period but more rapidly the lower the mass. B: the lower the mass, the smaller the phase difference. In all model objects, the phase difference increases with the oscillation period but more rapidly the higher the mass.
oscillation period. The dashed curves in Fig. 5
difference also depended on both the model weight and the
perature was not in time with air temperature. This phase
slowly oscillating changes in air temperature, the model tem-
perature contrasts with the phase advance between the oscilla-
tions of instantaneous temperatures and rates of change, but
changes identical to those of previous studies on arthropod
thermoreceptive cells (Ameismeier and Loftus 1988; Corbière-
Tichané and Loftus 1983; Ehn and Tichy 1996; Gingl et al.
2005; Loftus 1969; Loftus and Corbière-Tichané 1981), but
here we varied the oscillation period. This enabled us not only
to test the cold cell’s responsiveness to many different combi-
nations of instantaneous temperatures and rates of change, but
also to study the combined effect of both parameters on the
gain of the input-output function. We found that the gain can
be changed through changes in the duration of the oscillation
period. When the period is long, adaptation of the cold cell
performs a gain control function by improving the ability to
code the rate of temperature change at the expense of the
instantaneous temperature. As shown in Fig. 6, gain control in
the cold cell involves decreasing sensitivity to instantaneous
temperature while increasing sensitivity to the rate of change.
(The negative values for gain reflect the downward direction of
the temperature change, yielding a rise in impulse frequency,
and specify the receptor type—a cold cell).

The change in gain observed by changing the oscillation
period is summarized in Fig. 7. When temperature oscillates
with brief periods, the gain for the instantaneous temperature is
high but low for the rate of change; conversely, when tempera-
ture oscillates with long periods, the gain for the rate of
change is high but low for the instantaneous temperature.
Adaptation functions as a gain control mechanism. It permits a
high degree of precision at small values when it counts most,
without sacrificing the range of detection and without extend-
ing the measuring scale. Once the cockroach ventures from
under cover and into moving air, its superficial cold cell is
confronted constantly with temperature changes. In this situ-
ation, the fluctuation periods are brief. If the gain for the rate
of change is high, then impulse frequency will vary continually,
reflecting a succession of temperature changes. A cold cell will
be of advantage only if it contains a limit in the gain for the rate
of change. Without such a limit, the cell will always be
indicating temperature change because impulse frequency is
never steady. The amplitude of the temperature fluctuations
may be small, but it is never absent. A low gain for the rate of
change will improve the ability to signal the level of the actual
temperature. The animal will receive precise information about
the temperature value at which the change occurs and can seek
an area of different temperature. If the cockroach ventures back
under cover, the impulse frequency will become steady at some
low rate of temperature change whether up or down. In this
situation, the fluctuation periods are long. The cue will be that
impulse frequency begins to change at all. A high gain for the
rate of change will improve the ability to signal the threshold of
temperature change. Because of the high gain for the rate of
change, the cockroach will receive the early warning of slow
fluctuations or even creeping changes in temperature.

In this context, it should be noted that during slow and
continuous changes in air temperature, the temperature of the
receptive ending can be considered to be locked to the air
stream’s temperature. This is because the receptive ending is
positioned superficially within the sensillum peg, the sensillum

**FIG. 7.** Gain modulation by the duration of the oscillation
period. At brief periods, gain for instantaneous temperature is
high and for the rate of change low; at long periods, gain for
instantaneous temperature is low and for the rate of change
high.

**DISCUSSION**

The primary goal of this study was to determine the effect of
adaptation on the ability of the cockroach’s cold cell to code
information about the instantaneous temperature and the rate of
temperature change. We utilized oscillating temperature
changes identical to those of previous studies on arthropod
thermoreceptive cells (Ameismeier and Loftus 1988; Corbière-
Tichané and Loftus 1983; Ehn and Tichy 1996; Gingl et al.
2005; Loftus 1969; Loftus and Corbière-Tichané 1981), but
here we varied the oscillation period. This enabled us not only
to test the cold cell’s responsiveness to many different combi-
nations of instantaneous temperatures and rates of change, but
mass is $<10^{-7}$ mg, and the air stream is moving across the sensillum at $>10,000$ sensillum diameters per second. The phase difference between the oscillations in the discharge rate and temperature is not a matter of hysteresis; impulse frequency leads instantaneous temperature rather than lagging behind it. Impulse frequency has its counterpart mainly in the rate of temperature change as becomes manifested when their time courses are compared.

While sensillum temperature is virtually the same as air temperature, the temperature of small model objects departs considerably from air temperature. The extent of departure was expressed by two means: the transmission factor, which describes the temperature that the model reached during changes in air temperature, and by the phase difference, which indicates whether the former is in step with the latter. Clearly, the mass of the model objects affects both the transmission factor and the phase difference. The lower the model mass, the smaller the difference between the two temperatures and, in addition, the smaller the phase lags between them. Notwithstanding the difference between the dimensions of the model objects and the thermoreceptive sensillum, two properties are evident. First, the phase relationship between the oscillating temperature of the models and the oscillating air stream is negative due to hysteresis, but the phase relationship between the oscillating cold cell’s responses and the oscillating air stream is positive as result of its ability to respond to the rate of temperature change. Second, the sensillum temperature is locked to the air stream and takes on the maximum and minimum values of the oscillating air temperature. Thus sensillum temperature changes at the same rate as air temperature but with a positive phase shift. In the models, the temperature range covered during an oscillation period is smaller than air temperature. Thus object temperature changes at different rates than air temperature and with a negative phase shift.

The cold cell’s output cannot simply be defined in terms of the temperature input itself as some kind of passive transducer. Rather the output apparently reflects the cold cell’s ability to adjust its gain to different aspects of the temperature input. The signal controlling gain must be derived directly from the temperature input or from the signal of the cold cell itself. This inherently limits the accuracy with which gain can be controlled. The biophysical mechanism that allows the interaction of the incoming temperature parameters is unknown. This is not a trivial problem because, intuitively, the natural operation for a sensory cell to perform would be some kind of average or weighted sum not a product. Ultimately this gain control is part of what makes thermoreceptors so difficult to emulate with man-made devices.

**GRANTS**

This was supported by Austrian Science Fund Project P 20.196-B17.

**REFERENCES**


