courtship in *D. mercatorum*, although the existence of contact pheromones is highly probable since the courted male frequently taps the other male with his fore- and middle legs during their encounter.

The male may be first sexually stimulated by essential signals such as sex pheromone emitted by the female[11–13]. However, observations both in the laboratory and in the field suggest that the male, having once been excited, seems to try rather randomly to contact any individual that is near at hand. He is then capable of determining his proper sexual partner, mainly by using the sex pheromones as a clue. On the other hand, the male being courted by another male should be freed as soon as possible from annoying encounters and play his normal male role. This situation is also true for the male that improperly courts other males. Thus the courtship-inhibiting cues such as the chemical and the auditory ones are very useful under natural conditions in avoiding wasted time at feeding sites where many individuals assembled and mate.

[1] This work was supported by the special research project on instinct, University of Tsukuba. The author is most grateful to Dr and Mrs Hampton L. Carson for their kind reading of the manuscript.

2 Ewing, A. W., and Bennet-Clark, H. C., Behaviour *31* (1968) 288.
3 Ikeda, H., Takabatake, I., and Sawada, N., Behav. Genet. *10* (1980) 361.
4 Schilcher, F., von, Anim. Behav. *24* (1976) 622.
5 Miller, D.D., Goldstein, R. B., and Patty, R. A., Evolution *29* (1975) 531.
6 Bennet-Clark, H. C., Leroy, Y., and Tsacas, L., Anim. Behav. *28* (1980) 230.
7 Donegan, J., and Ewing, A. W., Anim. Behav. *28* (1980) 1289.
8 Ikeda, H., Behav. Genet. *6* (1976) 305.
9 Tompkins, L., and Hall, J. C., Z. Naturforsch. *36C* (1981) 694.
10 Tompkins, L., Siegel, R. W., Gailey, D. A., and Hall, J. C., Behav. Genet. *13* (1983) 565.
11 Tompkins, L., Hall, J. C., and Hall, L. M., J. Insect Physiol. *26* (1980) 689.
12 Venard, R., and Jallon, J.-M., Experientia *36* (1980) 211.
13 Tompkins, L., and Hall, J. C., Anim. Behav. *32* (1984) 439.

0014-4754/85/091197-03$1.50 + 0.20/0

The effect of head heating on the flight activity of the cockroach

J. Janiszewski

N. Copernicus University, Institute of Biology, Laboratory of Biophysics, 87-100 Toruń (Poland), 19 October 1984

Summary. Internal head heating restricted the flight activity in the cockroach *Periplaneta americana*. Heating the metathoracic ganglion did not have any pronounced effect on the flight. It is concluded that in the cockroach the head nervous centers are very heat-susceptible and might be the coordinating center for temperature responses.

Key words. Periplaneta americana; head temperature; flight activity.

Studies performed on homeotherms have given evidence that in the exercising animal the brain is the part of the body most protected against overheating[1–5]. From the point of view of comparative physiology it is interesting that also in the honeybee *Apis mellifera* the ability to fly at air temperatures up to 46 °C is accompanied by a very effective head cooling mechanism[6,7]. However, most insects must limit their activity to avoid overheating in a hot environment[8]. This is particularly true of species which do not exhibit any physiological thermoregulation, for example the American cockroach *Periplaneta americana*[9]. The aim of the experiments presented was to verify whether increased head temperature was a limiting factor for flight in *P. americana*.

Materials and methods. The experiments were performed on adult males of the American cockroach *Periplaneta americana* weighing 997 ± 12.53 mg. The insects were kept under natural photoperiod at 28–30 °C and 55–65% relative humidity. They were fed on a diet of apples, porridge and water ad libitum.

Thermodes made from loops of enamel-insulated constantan wire, 0.05 mm in diameter, were used for internal body heating. The loops were extended by copper leads to a DC power supply unit. The body was heated as the current flowed through the high-resistance constantan wire. The temperature of each thermode was measured by a thermocouple fixed to it with polyethylene glue. The copper-constantan thermocouples were made from wires 0.05 mm in diameter. They were calibrated with the use of a Beckman thermometer and a digital nanovoltometer (type 180, Keithly Instr. Inc., USA). During the experiments the temperature was recorded on a Speedex Recorder SP-G7P (Riken-Denshi Co. Ltd., Tokyo, Japan). Its sensitivity was 0.089 °C per 1 mm pen deflection. The measuring system was calibrated by means of a reference voltage from a thermocouple placed in a water thermostat, which stabilized the temperature at ± 0.05 °C.

The thermode/thermocouple pairs were implanted into the animal from its dorsal side, the first one 3 mm deep into the head and the other into the metathorax near the ganglion. They were fixed with Taki Wax.

After the implantation only cockroaches which flew well were used for experiments. Ten were selected out of 15. The selected insect was placed in chamber (70 × 50 × 50 cm), which was heated with a warm air stream. The temperature in the chamber (recorded by the thermocouple) was stabilized at 28.4 ± 0.06 °C. In the chamber the animal stayed at rest for about 30 min. After that time it was forced to fly, as the body lifted on the thermocouple leads had no contact with the ground. When the wing motion stopped, the insect was set down for a second and then lifted again, which acted as a stimulus to continue the flight. Every stimulus was automatically recorded on a tape recorder. The stimulation was stopped when no response was observed. The maximal time for stimulation was 10 min. The flight was not interrupted if it was continued after the 10th min; only after the cessation of flight was the animal set down.

The body heating started immediately after the animal had been placed in the chamber and followed at a rate of 0.6 °C/min. After the desired level had been reached, the temperature was stabilized.

The following parameters were used to describe flight activity of the cockroach: 1) frequency of stimulation, 2) period of positive responses to stimulation – later called 'duration of flight', 3) maximal increase of thorax temperature (MTT).

Each experimental series was performed on 10 insects. For each calculated parameter the mean values and standard errors are shown.

The experiments were conducted during the day time.

Results. Control. When neither the head nor the thorax was heated the cockroaches had to be stimulated to flight 4.8 ± 1.4

times/min (fig. 1). During the flight the MTT was 6.9 ± 0.3 °C (fig. 1). The mean duration of flight was 10.05 ± 0.35 min (fig. 2).
Head heating. The head was heated to mean temperatures 32.4 ± 0.05, 36.1 ± 0.12 and 40.1 ± 0.13 °C. Stimulation frequency increased in parallel with head temperature (fig. 1). At the same time the MTT (fig. 1) and the duration of flight (fig. 2) decreased. The changes in all these parameters indicate restriction of flight activity effected by head heating.

Thorax heating. Heating the head to 40.1 ± 0.13 °C almost totally suppressed the ability to fly. To see to what extent the effect of the temperature of the head is specific, a series of experiments was performed, in which the close surroundings of the methathoracic ganglion were heated to 40.3 ± 0.33 °C. The results obtained showed that the values of both the stimulation frequency (fig. 1) and duration of flight (fig. 2) did not differ significantly from those in the control. The MTT was not calculated.

Discussion. Although in the last decade much experimental work has been done on the mechanisms of insect thermoregulation[8, 10], there are only few data on the neural control of the described phenomena. The following questions should be answered; is there any definite neural center for thermoregulation, and if so, where is it located?

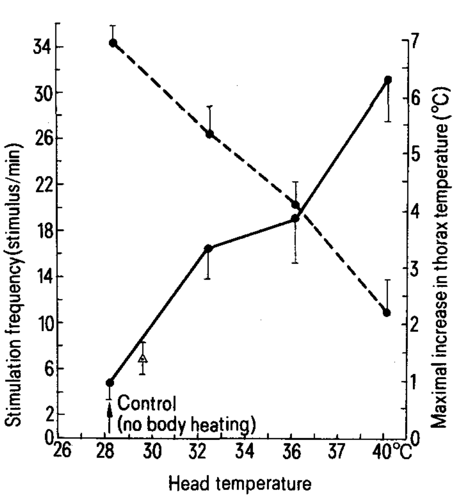

Figure 1. Stimulation frequency to evoke flight —— and maximal increase in thorax temperature during flight ---- in *P. americana* with heated head. △ indicates stimulation frequency in insects with the metathorax heated to 40.3 ± 0.33 °C and no head heating. Stimulation frequency and maximal increase in thorax temperature under control conditions (no body heating) are indicated by an arrow. Mean values and SE are indicated. n = 10.

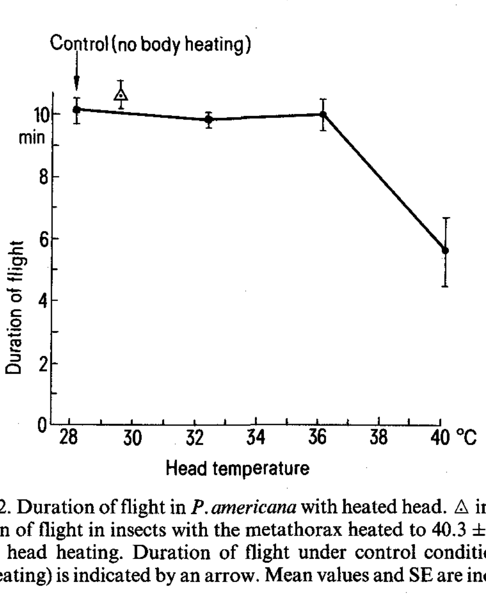

Figure 2. Duration of flight in *P. americana* with heated head. △ indicates duration of flight in insects with the metathorax heated to 40.3 ± 0.33 °C and no head heating. Duration of flight under control conditions (no body heating) is indicated by an arrow. Mean values and SE are indicated. n = 10.

As already indicated in the preliminary studies[9], the results presented in this paper showed that raising the head temperature was limiting the flight activity, which could be explained as avoidance of lethal body overheating by muscle thermogenesis. Because heating the metathoracic ganglion to a relatively high temperature (40.3 ± 0.33 °C) did not have any pronounced effect on the flight, it might be concluded that although temperature-sensitivity of this ganglion does exist[11], it is not involved in temperature regulation. If so, the site of temperature regulation in the cockroach might be located in the head. This hypothesis is supported by the observation on wing-beat frequency in *P. americana*[12]. During the warm-up portion of flight, there was no appreciable increase in wing-beat frequency even though the pterothorax temperature increased approximately by 1.5–3.5 °C. Farnworth[12] concluded that the wing-beat frequency center may be outside the pterothorax, perhaps in the head or prothorax. Indeed, not only the head but also the prothoracic ganglion must be considered as sites of temperature regulation in *P. americana*. Murphy and Heath[13] investigated the spontaneous activity of neurons in that ganglion. They found several highly temperature-sensitive cells and suggested that they might be central temperature receptors.

The significance of head temperature for thermoregulation under hyperthermia has only been investigated in detail in *P. americana* and in the honeybee *Apis mellifera*[6, 7]. When the heads of tethered bees were heated up to 46 °C they regurgitated nectar from their honey crop and held it on the 'tongue'. That prevented the head temperature from rising and stabilized it. In flying bees the cooled head served as a heat sink for excess heat from the thorax. Because thoracic heating to near lethal temperatures did not result in droplet extrusion from the mouth, Heinrich[7, 14] concluded that the head is a high-temperature sensor in honeybees. It is of interest that it has also been reported that the sphingid *Pholus achemon* extrudes a drop of liquid from its proboscis when overheated[15]. Unfortunalely the authors did not measure in head temperature.

In *Periplaneta americana* no fluid extrusion was observed. Therefore evaporative cooling could not be significant; probably most of the heat is lost by convection. However, convective cooling, even increased by wing-movement, could not be effective enough and behavioral thermoregulation is dominant.

1 Taylor, C.R., and Lymann, C.P., Am. J. Physiol. *222* (1972) 114.
2 Clough, D.P., and Jessen, C., Pflügers Arch. *347* (1974) 235.
3 Baker, M.A., and Chapman, L.W., Science *195* (1977) 781.
4 Chesy, G., Caputa, M., Kadziela, W., Lachowski, A., and Kozak, W., in: Satellite of 28. Int. Congress of Physiol. Sci. Pécs, p. 193. Eds Z. Szelényi and M. Székely. Akadémiai Kiadó, Budapest 1980.
5 Caputa, M., Kadziela, W., and Narebski, J., J. therm. Biol. *8* (1983) 265.
6 Heinrich, B., Science *205* (1979) 1269.
7 Heinrich, B., J. exp. Biol. *85* (1980) 61.
8 Casey, T.M., in: Insect thermoregulation, p. 79. Ed. B. Heinrich. John Wiley and Sons, New York 1981.
9 Janiszewski, J., J. therm. Biol. *9* (1984) 177.
10 Kammer, A.E., in: Insect thermoregulation, p. 115. Ed. B. Heinrich. John Wiley and Sons, New York 1981.
11 Kerkut, G.A., and Taylor, B.J.R., Nature *178* (1956) 426.
12 Farnworth, E.G., J. Insect Physiol. *18* (1972) 359.
13 Murphy, B.F., and Heath, J.E., J. exp. Biol. *105* (1983) 305.
14 Heinrich, B., J. exp. Biol. *85* (1980) 73.
15 Adams, P.A., and Heath, J.E., J. Res. Lepidoptera *3* (1964) 69.

0014-4754/85/091199-02$1.50 + 0.20/0