

TEMPERATURE REGULATION OF THE SPHINX MOTH, *MANDUCA SEXTA*

II. REGULATION OF HEAT LOSS BY CONTROL OF BLOOD CIRCULATION

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INTRODUCTION

The way in which some sphinx moths maintain a stable elevated thoracic temperature (T_{Th}) during flight when ambient temperature (T_A) varies has not been shown. In the sphinx moth, *Manduca sexta*, however, blood circulation has been implicated in the transfer of heat from the thorax to the abdomen during free flight (Heinrich, 1970a). The present study undertakes to examine in greater detail the relation of blood circulation to body temperature in this species.

Blood circulation in insects functions in the distribution of metabolites. In contrast to the situation in vertebrates, the blood of insects is not involved in the transfer of respiratory gases and has hitherto not been demonstrated to be important in temperature regulation. It is, therefore, not surprising that rapid blood circulation is not of vital importance to many insects. Grasshoppers with the abdomen removed have been observed to beat their wings for an hour or more (D. M. Wilson, personal communication), and cockroaches appear to live normally after the heart is excised (F. Engelmann, personal communication).

Descriptive knowledge of the insect circulatory system dates back to Harvey (1628) and has been reviewed repeatedly (Beard, 1953; Richards, 1963; Jones, 1964; Chapman, 1969). This circulatory system is an 'open' one although a pulsatile organ which aids in the circulation of blood is located dorsally usually along the full length of the animal. In moths, and in most other insects, this so-called heart is a simple tube which extends along the mid-dorsal line of the abdomen and into the thorax where it is then called the aorta. Contractions of the heart proceed usually from posterior to anterior but may be reversed on occasion. In several orders (see Wigglesworth, 1965 and Bullock & Horridge, 1965) including the Lepidoptera (McIndoo, 1945) the heart is known to be segmentally innervated from the ventral nerve chord. The functional significance of this innervation has in no case been established conclusively.

Temperature regulation by blood circulation is feasible if small amounts of blood transfer large quantities of heat; and when the site from which heat is transported is at a much higher temperature than that from which it is dissipated to the environment. A large excess of body temperature over ambient temperature (ΔT) is not achieved

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by most insects which are small, poorly insulated and engage in maximum metabolic rates for only short periods. Most sphingids, however, are large and heavily insulated and can maintain a substantial ΔT during free flight (Heinrich, 1970*b*). Furthermore, they feed, oviposit, and seek mates while in flight so that periods of heat production are often prolonged, and convective heat loss from the thorax alone during sustained flight at high ambient temperature is not always sufficient to prevent overheating.

METHODS

Abdominal temperatures (T_{Ab}) were measured by inserting a sharpened 30 gauge copper-constantan thermocouple under the integument through the intersegmental membranes. These measurements were made immediately after free flight at 15 and 35 °C. Temperatures were registered on a recording potentiometer.

Local heating was carried out by pinning moths by their wings on to a frame of balsa wood so that their bodies were freely suspended. A narrow beam of light from an incandescent lamp was directed either on to the thorax or on to the abdomen while body temperatures and heart pulsations were continuously monitored from both the thorax and the abdomen.

The heart pulsations were monitored with silver electrodes which were implanted on each side of the vessel. The electrodes were wired to a pair of Biocom impedance converters, whose signals were recorded on separate channels of a polygraph. Impedance changes resulted from variations of the distance between the electrodes, or from changes in electrical conductivity across the vessel when fluid passed through it. Usually the electrodes were firmly held in place by small exudates of blood which had dried around them. The impedance measurements recorded not only the timing of the heart pulsations; they also indicated the relative amplitude of these movements.

Body temperatures of stationary moths were measured with 40 gauge copper-constantan thermocouples inserted into the muscles of the thorax and under the integument in the abdomen. The thermocouple leads were connected to a multi-channel potentiometric recorder.

RESULTS

Anatomy

The dorsal vessel (heart) of *M. sexta* extends along the mid-dorsal line throughout the length of the abdomen (Fig. 1). The vessel is clearly visible beneath the transparent tergites when the dorsal scales are removed (see photograph, Heinrich, 1970*a*). Segmentally arranged pairs of ostia allow inflow of blood, and ostial valves prevent outflow (see Gerould, 1938). The blood is driven through the heart by peristaltic contractions which proceed from the posterior end of the abdomen into the thorax (see Brocher, 1919). The vessel makes a loop in the thorax (Fig. 1) through the dorsal longitudinal muscle (indirect wing depressor). This loop is absent in many Lepitoptera. It has previously been reported in sphinx moths (Burgess, 1881; Brocher, 1919) and in certain bees (Wille, 1958).

The blood flows into the ventrum of the abdomen after being pumped through the thorax. Continued motion of the blood is there facilitated by undulations of the ventral

diaphragm (see Richards, 1963). In dissected preparations of *M. sexta* the posterior-lateral movements of the ventral diaphragm are continuously maintained.

Most of the abdomen is filled with air sacs (Fig. 1), but their volume varies depending on whether or not the moths have a full stomach and are carrying eggs.

The muscles of the thorax are separated from the abdomen by a gas-filled space (Fig. 1). Since T_{Th} is much higher than T_{Ab} during flight, heat should reach the abdomen from the thorax by conduction, although this gas-filled space should minimize it. In addition to being insulated from conductive heat loss to the abdomen by this hollow space, the thorax of this species is insulated from convective heat loss to the air by a thick (2 mm) layer of thoracic scales. The abdomen, however, is lightly (0.5 mm) insulated.

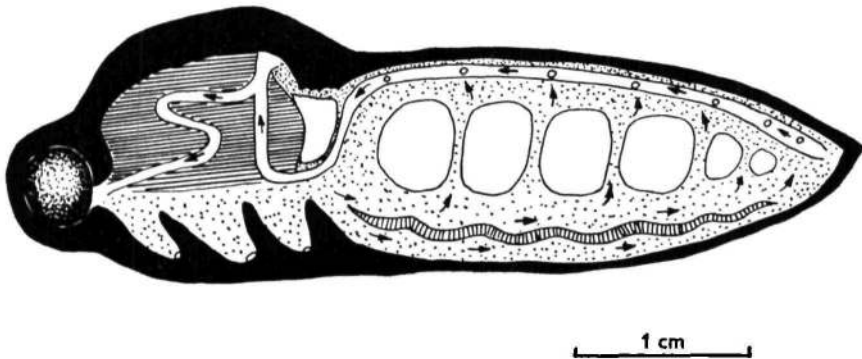


Fig. 1. Schematic diagram of sagittal section of *M. sexta* showing anatomical features related to temperature regulation. Solid black, insulative scales. Horizontal cross-hatching, dorsal longitudinal muscle. Vertical cross-hatching, ventral diaphragm. Note air sacs in abdomen and hollow space between thorax and abdomen. The dorsal vessel (heart) is situated close to the dorsum of the abdomen. Note the lateral ostia of the heart. Arrows indicate direction of blood flow.

Abdominal temperatures immediately after free flight

It is impractical to make direct measurements of the volumes of blood circulating through the thorax and the abdomen during free flight. However, indirect measurements of blood flow can be made from the distribution of temperatures in the abdomen. Since the blood normally flows anteriorly from the dorsal abdominal vessel into the thorax and then flows out of the thorax into the ventral part of the abdomen (see Fig. 1), the difference of temperature between the dorsum and the ventrum should be a function of the rate of blood flow. Measurements of T_{Ab} taken immediately after flight at different T_A can thus be used as an indication of differences in rate of blood flow.

The temperature of the dorsum of the abdomen approaches T_A during flight. However, the blood entering the ventrum of the abdomen from the thorax should initially be close to T_{Th} . Therefore, if the flow of blood from the dorsum of the abdomen, through the thorax and into the ventrum of the abdomen were the same during flight at all T_A , the difference in temperature between the thorax and T_A should be related to the difference in temperature between the dorsum and the ventrum of the abdomen. For example, T_{Th} remains near 41 °C during flight at both 15 and 35 °C (Heinrich, 1970a). Therefore, if one assumes a constant blood flow, there

should be a large dorso-ventral temperature difference (max. 26 °C) in the abdomen during flight at a T_A of 15 °C and a small difference (max. 6 °C) during flight at a T_A of 35 °C. However, as shown in Fig. 2, the dorso-ventral difference in abdominal temperatures is small (about 2 °C) at 15 °C and relatively large (about 4 °C) at 35 °C. These data therefore suggest that the volume of blood moving between thorax and abdomen during flight is very small at a T_A of 15 °C and comparatively large at a T_A of 35 °C.

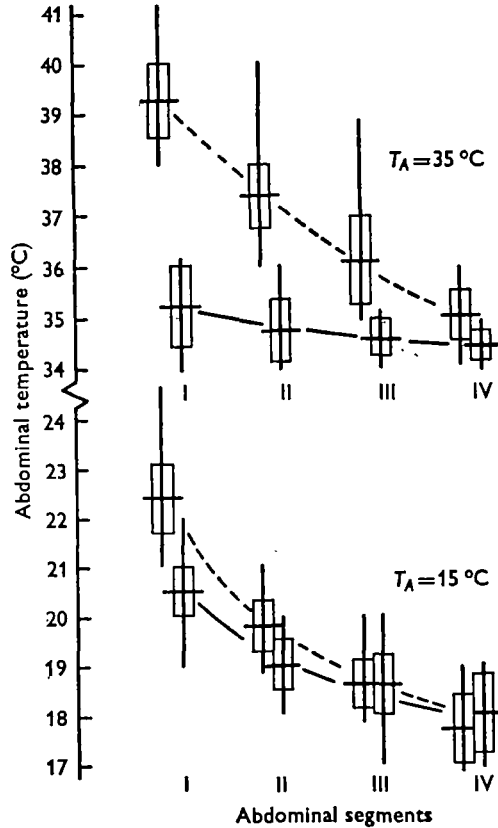


Fig. 2. Abdominal temperatures immediately after free flight. Measurements were taken in the dorsum (solid lines) and ventrum (broken lines) of segments I-IV within about 7 s after capture during flight at 35 and 15 °C. Each box encloses the 95 % confidence interval derived from 10 measurements. The vertical lines represent the range. Each animal was used only once, and no more than four measurements were taken from each animal.

Control of the blood circulation

Regulation of T_{Th} could clearly involve blood circulation. However, stabilization of T_{Th} could conceivably be achieved automatically by the pumping of the heart in the abdomen at a rate dependent on abdominal temperature. To test whether the pumping of the heart into the thorax passively follows T_{Ab} or whether it is determined by the temperature of the thorax, heat was applied exclusively to the thorax (see *Methods*).

When the thorax was heated at an initial rate of 2-4 °C/min, T_{Ab} at first remained constant. Large-amplitude pulsations of the abdominal heart were observed through

the transparent tergites when T_{Th} reached 40 °C or above. The frequency and amplitude of these pulsations increased as T_{Th} increased (Fig. 3). They were at maximum rate and amplitude when T_{Th} was 44–45 °C. In this range of T_{Th} the pulsations were always at regular intervals and always travelled from abdomen to thorax. When T_{Th} was below 35 °C, however, there were often intervals without pulsations, and periods during which pulsations travelled from anterior to posterior. The results of these experiments suggest that pumping of the heart in the abdomen is controlled, at least in part, by the temperature of the thorax.

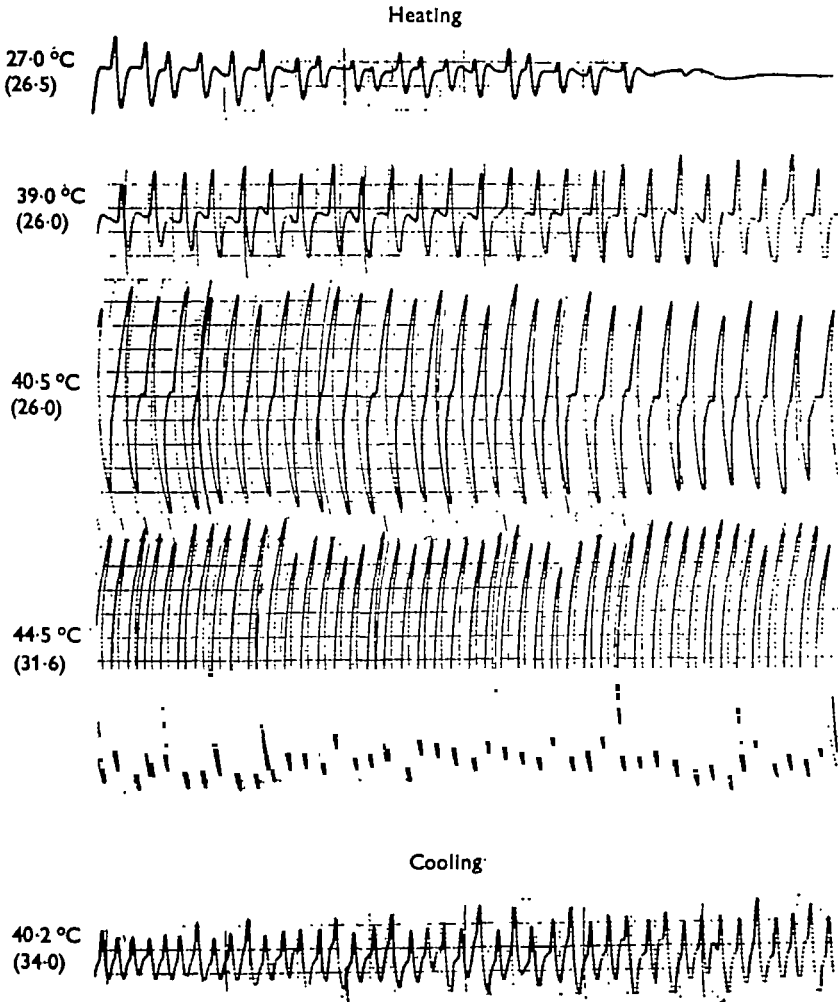


Fig. 3. Records of impedance changes during pulsations of the heart while the thorax was heated and subsequently cooled. The numbers indicate T_{Th} and T_{Ab} . The recordings, lasting 15 s, were taken from the second abdominal segment.

The maximum rates of pumping of the abdominal heart during intense heating of the thorax were dependent not only on thoracic, but also on abdominal, temperatures. For example, the maximum rates of high-amplitude pulsations that could be invoked when the thorax was intensely heated were about 90 beats/min when T_{Ab} was 16 °C,

170 beats/min when T_{Ab} was 26–27 °C and 210 beats/min when T_{Ab} was 39 °C. However, the amplitude of the pulsations of the abdominal heart during heating of the thorax appeared to be as large at a T_{Ab} of 15 °C as at a T_{Ab} of 25 °C or above.

When the abdomen was heated, contractions of the heart increased in rate but their amplitude sometimes decreased (Fig. 4). The movements of the vessel, which were vigorous at lower T_{Ab} , were often no longer visible when T_{Ab} was 40 °C or above. The heart appeared to become constricted, although there were sometimes brief bursts of high amplitude pulsations (often anterior to posterior).

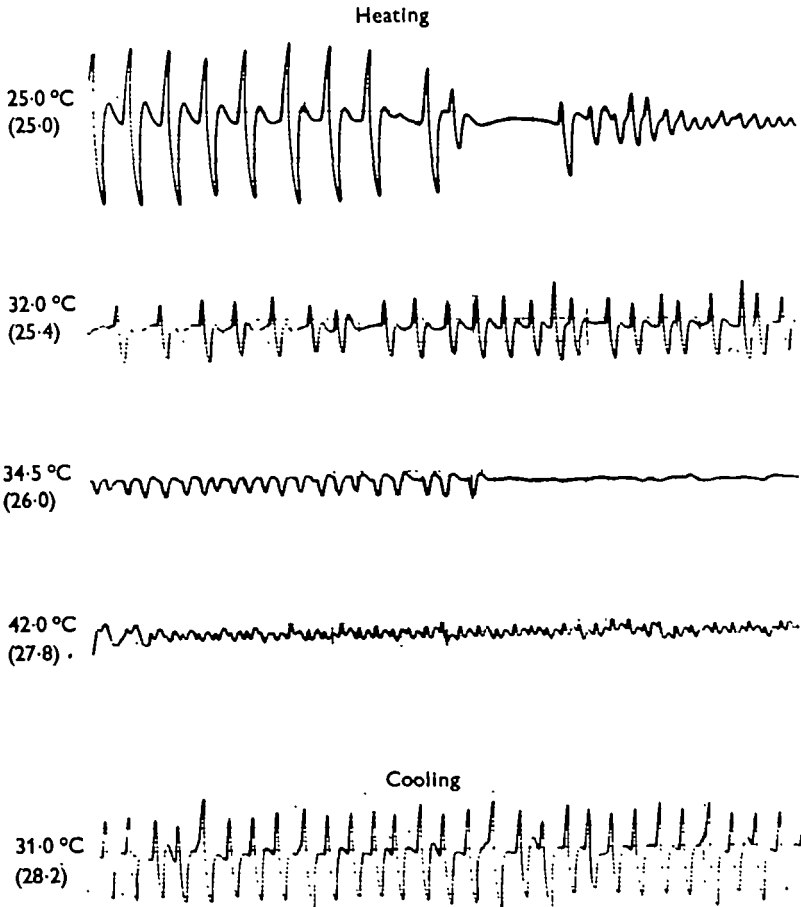


Fig. 4. Pulsations recorded from the heart during heating of the abdomen. These recordings are from the same animal as those of Fig. 3 and the electrodes were still in the same place. The records span 15 s. The numbers indicate T_{Ab} and (T_{Th}).

The pulsations were always at the same frequency, and appeared to be of the same amplitude, in the thorax and in the abdomen, even though the difference in temperature between the thorax and the abdomen was as much as 18 °C (Fig. 5).

When the ventral nerve cord was transected at the second abdominal segment the pulsation rates of the heart were reduced and thoracic temperature no longer affected frequency of pulsations (Fig. 5). The pulsation rate of the heart in operated animals did

not exceed 40–50 beats/min even when the thorax was heated to over 40 °C at a T_{Ab} of 24–25 °C (Fig. 6). It is therefore suggested that impulses from the thorax via the ventral nerve cord affected pulsations of the heart in the abdomen.

In animals with transected nerve cord, pumping rates of the abdominal vessel were strongly influenced by abdominal temperature and, in contrast to intact moths, reduction in amplitude was not observed (Fig. 5). Therefore, the pulsations of the abdominal heart in moths with transected nerve cord can be affected by abdominal temperature. In the intact moth, however, the rate, amplitude, direction and duration of the pulsations appeared to be modulated by impulses from the thorax via the ventral nerve cord.

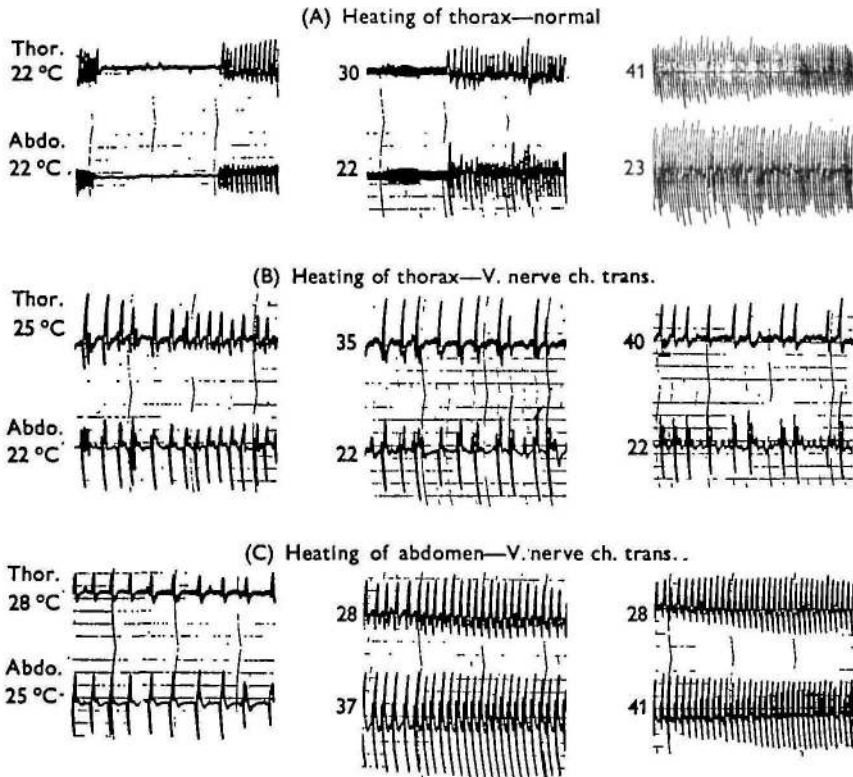


Fig. 5. Electrical impedance recordings simultaneously from the thorax (upper traces) and from the second abdominal segment (lower traces). All of the recordings are derived from the same moth. The amplification and position of the electrodes were not changed throughout A, B or C. T_A was 22 °C. Thoracic temperature and T_{Ab} are indicated at the side of each record spanning 32 s. (A) Thoracic heating of the normal moth. (B) Heating of the thorax after the ventral nerve cord was transected. (C) Heating of the abdomen after the ventral nerve cord was transected.

The abdomen as a heat exchanger

Temperature changes in the thorax and in the abdomen, and pulsations of the heart and aorta, were also recorded during heating of the thorax. The increase in T_{Ab} , the levelling of T_{Th} , and the onset of high-amplitude pulsations of the abdominal heart were closely correlated. This suggests that the blood carries heat from the thorax to the abdomen, which acts as a heat exchanger. Thoracic temperature of the

artificially heated animals (on thorax) usually stabilized near 42°C while the abdominal temperature still increased. If the heat input was not excessive, T_{Ab} stabilized at a temperature intermediate between T_{Th} and T_A (Fig. 7). Under these circumstances, fluctuations of T_{Th} were clearly correlated with changes in the pulsations of the abdominal heart (Fig. 8). When the pulsations stopped, T_{Th} immediately increased and when the pulsations resumed, T_{Th} again declined and stabilized. Dead animals, or those with transected ventral nerve cord, did not show an increase in T_{Ab} during heating of the thorax (Fig. 11).

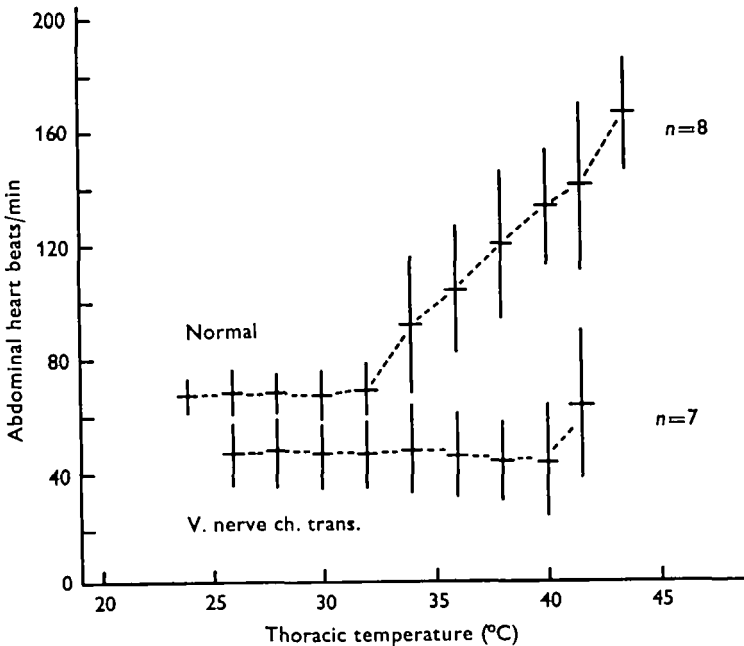


Fig. 6. Pulsation rates of the heart in the second abdominal segment during application of heat to the thorax of normal moths and of moths with transected ventral nerve cord. The vertical lines represent the 95% confidence intervals. Ambient temperature was $24-25^{\circ}\text{C}$.

If the input of heat to the thorax was excessive, the moths were unable to stabilize T_{Th} . Under these circumstances T_{Ab} continued to increase along with T_{Th} (Fig. 9) and the pulsation rate and amplitude appeared to be maximal. The difference between T_{Th} and T_{Ab} remained relatively constant.

When the thorax was artificially heated, the ventrum of the abdomen (measured in the second abdominal segment) reached a higher temperature than the dorsum. Furthermore, the dorsum was nearly the same temperature throughout its length (Figs. 7, 9). The observations of T_{Ab} immediately after free flight are similar (Fig. 2). These abdominal temperatures are consistent with predictions of T_{Ab} which could be based on the course of blood circulation (see Fig. 1). The distribution of T_{Ab} is not explicable in terms of heating by conduction from the thorax. For example, the same elevated temperature (above T_A) in the dorsum of the second and fifth abdominal segments (see Figs. 7, 9) would not be possible if the increase in temperature of the abdomen during thoracic heating were due to conduction of heat from the thorax,

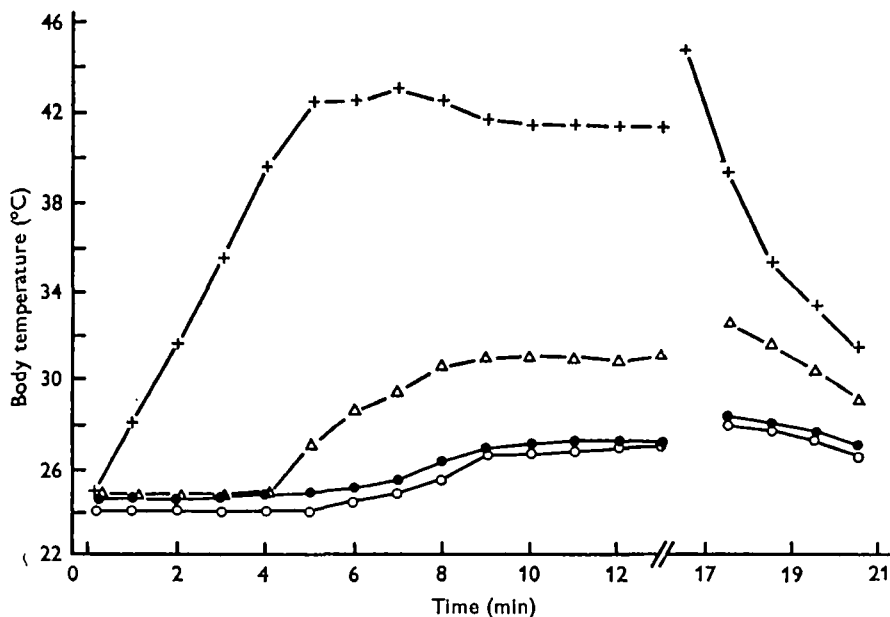


Fig. 7. Body temperature changes during the application of heat to the thorax, and during the subsequent cooling. +, Thorax; Δ abdominal second segment ventral; ●, abdominal second segment dorsal; ○, abdominal fifth segment dorsal.

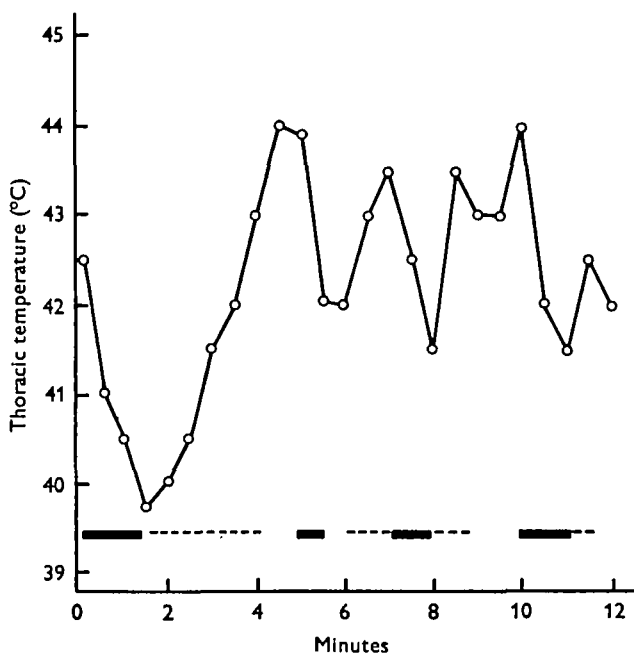


Fig. 8. The correlation of full-length pulsations of the abdominal vessel and T_{T_h} during the application of heat to the thorax. This moth, unlike most, did not have continuous pulsations of the heart. There were periods during which movements ('fibrillations') of the vessel were visible only in the anterior portion. The fluctuations of T_{T_h} during the constant application of heat to the thorax were unusually large. ----, Fibrillations in anterior of heart; —, full length pulsations.

The temperature in the ventrum of the second abdominal segment is up to 9 °C higher than in the dorsum (Fig. 9). It therefore appears that the blood has lost most of its heat when it has entered the dorsal vessel. It is then impelled into the thorax with only minor further temperature changes.

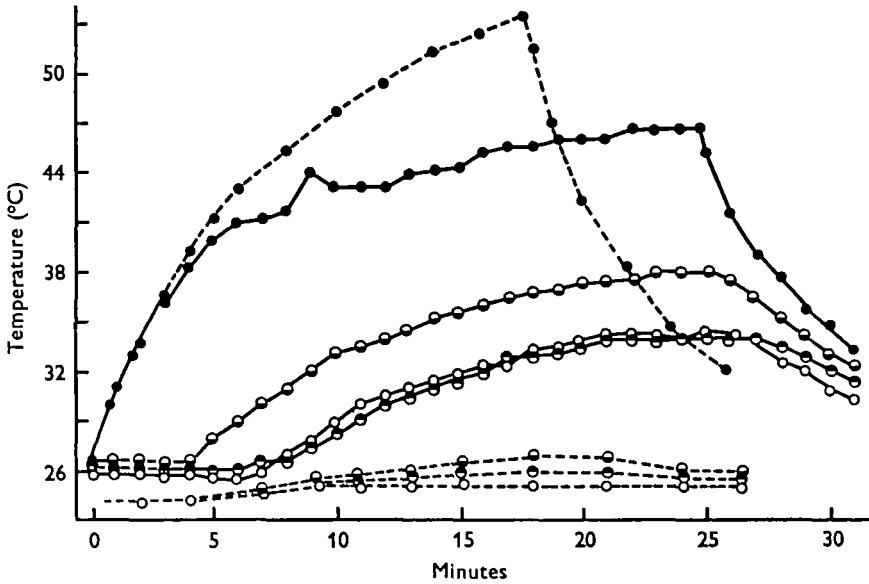


Fig. 9. Body temperature changes during and after the application of heat to the thorax. The four solid lines represent temperature changes in the live moth, and the four broken lines indicate the temperature changes recorded from the same four thermocouples still in place after the moth was killed and heated as before. ●, Thorax; ⊖, ventrum of second abdominal segment; ⊕, dorsum of second abdominal segment; ○, dorsum of fifth abdominal segment.

DISCUSSION

Continuous flight is obviously of great biological importance to sphingids which extract nectar from flowers while hovering. In order to hover, a high metabolic rate and a high body temperature are presumably necessary. Sphingids for the most part are active at night, and are essentially non-stop flyers in the wild. These adaptations minimize their options for behavioural temperature regulation (see Clench, 1966). They have therefore probably experienced more selective pressure to develop physiological temperature regulation during flight than most diurnal insects.

The type of temperature regulation found in *M. sexta* during free flight is energetically economical in as much as it may involve only negligible energy expenditure above that which is needed to operate the flight motor. It utilizes anatomical features which are only slightly modified from those already existing in most other insects (see Wigglesworth, 1965): (1) a dorsal vessel which pumps blood into the thorax; (2) an aorta modified to go through the flight muscles; (3) a ventral diaphragm; (4) a separation of thorax from abdomen; (5) a covering of scales over the body; (6) an open circulatory system in which blood flows close to the integument and over the air sacs. Thoracic temperature regulation by blood circulation does require, however, a high degree of co-ordination of the heart musculature, which necessarily involves a complex

integration of its circular, longitudinal and alary muscles. In the silkworm, *Bombyx mori*, the heart is innervated from the ventral nerve cord (McIndoo, 1945); a similar situation may be found in *Manduca*. In some species of insects the heart is myogenic (Yeager, 1939; McCann, 1965) although neurogenic control can be superimposed (Smith, 1968) and hormones can also affect its activity (Davey, 1963). Action potentials recorded from the moth myocardium resemble those generally associated with the myocardia of higher animals (McCann, 1963). Although it is generally recognized that the blood of insects is functional in the transfer of nutrients, waste products, hormones, etc. it has not been shown that it is also functional in the transfer of heat for temperature regulation. Except for the latter, these functions do not require rapid response of the heart. A functional significance for neural control of the heart *per se* has not previously been established (see Jones, 1964). However, the data presented in the present paper indicate that it is essential for temperature regulation by blood circulation.

In the laboratory, under confined conditions where the moths have difficulties in engaging in continuous flight, they sometimes maintain an elevated T_{Th} by on-off shivering responses (see Adams & Heath, 1964). This pattern has apparently not been reported under field conditions where the moths can engage in continuous flight.

Temperature regulation involving the transfer of heat by the blood to the abdomen presumably occurs during continuous flight at high T_A when the moths are uninterruptedly producing endogenous heat. Moths without active circulation could sustain flight only in a very narrow range of T_A (*c.* 6 °C) at which T_{Th} was still appropriate for flight. However, with the circulatory system intact, flight was observed over a range of T_A spanning 23 °C (Heinrich, 1970a). In the present investigation exogenous heat was applied to the thorax while the moths were at rest. It remains to be determined whether or not the same volumes of blood are pumped into the thorax under these conditions. Differences in the circulatory performance of freely flying and stationary moths which are heated may be expected. For instance, there are differences in blood pressure depending upon whether or not the insect is active (see Bayer, 1968) which could secondarily affect flow rates.

At present there are no direct measurements from which to determine the volumes of blood that are pumped by the insect heart. It is possible, however, to calculate the minimum volumes of blood that must be pumped for the circulatory system to dissipate the heat produced in the thorax and the maximum volumes of blood that the heart should be capable of pumping, if the following simplifications and assumptions are made: (1) the specific heat of blood is 1.0; (2) the blood is heated to T_{Th} in the thorax and cooled to T_A in the abdomen; (3) each c.c. of O_2 consumed yields 4.7 calories; (4) during flight the amount of metabolic heat produced by tissues other than the flight muscles is relatively small and insignificant.

The oxygen consumption of a 2.0 g *M. sexta* during free flight is *c.* 45 c.c. O_2 /g h which yields *c.* 7.0 cal/min. The minimum volume of blood which would have to be pumped through the thorax and abdomen will depend on the difference in temperature between thorax and abdomen. For example, if the ΔT were 1.0 °C, 7 c.c. of blood/min would be required, and if ΔT were 10 °C, then 0.7 c.c. would be needed (see Fig. 10). A few hundredths of a c.c. of blood/min pumped through the thorax when ΔT is 25–30 °C could result in a reduction of several degrees in T_{Th} . However, the volume

of blood necessary to maintain T_{Th} stable when ΔT is small would require prohibitively high rates of flow. Nevertheless, in the average range of ΔT observed experimentally (8–26 °C) a flow of less than 1 c.c./min would allow T_{Th} to remain at typical levels if heat transfer were 100% efficient.

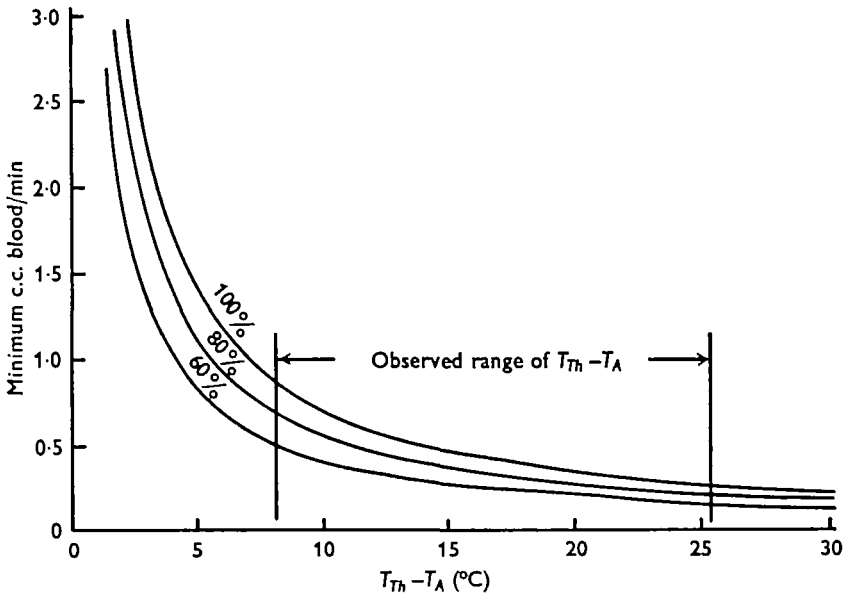


Fig. 10. The minimum volumes of blood that must be pumped through the thorax at different ΔT if the stabilization of T_{Th} were by blood circulation only. The three lines represent the volumes required if 100, 80 or 60% of the total calories expended were converted to heat.

The dorsal vessel in the abdomen is about 30 mm long and varies in diameter from about 0.25 to 1.0 mm. Assuming that the average inside diameter is about 0.5 mm then its volume ($\pi r^2 l$) is about 0.006 c.c. When the rate of pulsations is 180/min then 1.08 c.c. of blood/min are pumped into the thorax if the vessel is to be emptied with each pulsation. Under the conditions stated, this volume of blood is more than the minimum required to dissipate 7 cal/min from the thorax when T_A is 35 °C and T_{Th} is maintained at 43 °C. These calculations indicate, therefore, that temperature regulation, observed in *M. sexta* by circulatory control, is physically reasonable.

However, the actual percentage of the total heat lost from the thorax by circulation may be low and insignificant when the moths are conserving heat in the thorax, as during flight at low T_A . The number of calories lost from the thorax by convection, conduction and evaporation has not yet been determined, but it is possible to estimate magnitudes. For example, approximately three times as much heat would be lost from the thorax by conduction and convection during flight at 16 °C, when ΔT is about 24 °C, than during flight at 35 °C when ΔT is about 8 °C.

The rate of evaporative cooling is related to saturation deficit, which was greater at high T_A . Passive evaporative cooling should therefore have been greater at high T_A than at low. Church (1960) found that evaporative cooling during flight in *Bombus*, *Triphaena* and *Schistocerca* did not cause a reduction in T_{Th} of more than 1.0 °C. If the reduction of T_{Th} from 24 to 8 °C during flight in *M. sexta* were accomplished by

evaporative cooling from the thorax, and the evaporation of 1 mg water dissipates 0.585 cal, then using the assumptions listed previously, about 480 mg of water/h $[(24-8)/24 (7 \text{ cal/min}) (0.585)^{-1} 60]$ must be lost from the thorax. In a large (2 g) *M. sexta*, this would be 24% body weight loss of water/h. Combined with the evaporative water loss which may also be occurring from the abdomen, the total rate of water loss would appear to be excessive if it were sustained for the typically prolonged durations of flight in sphingids. At the present time, however, there are no data either giving the amount of water lost from the thorax during flight at any temperature, or demonstrating evidence for a mechanism whereby the flow of air through the thorax is regulated with regard to temperature regulation during flight. It is apparent, however, that in *M. sexta*, because of passive heat loss from the thorax at both high and low T_A , the heat produced in the thorax is never dissipated exclusively by the circulatory system.

It can be concluded that the stabilization of T_{Th} allows *M. sexta* to fly in a wide range of T_A . The circulatory mechanism of temperature regulation, which may be the major factor in regulation of thoracic temperature in *M. sexta*, is economical from the standpoint of energetics and water economy in as much as it appears not to require heat production, or water loss, beyond other requirements unrelated to temperature regulation.

SUMMARY

1. The circulatory anatomy of *Manduca sexta* is such that heat loss from the thorax is minimized when the flow of blood is reduced, and maximized when it is increased.

2. Abdominal temperatures immediately after flight suggested that blood flow was substantially increased during flight at high T_A , and greatly reduced during flight at low T_A .

3. When the thorax was artificially heated, the pulsation rates of the abdominal blood vessel increased, the amplitudes of the pulsations became large, and the pulsations were always in the posterior-anterior direction.

4. Heating of the abdomen often resulted in the constriction of the abdominal vessel and a reduction in the amplitude of the pulsations.

5. Transection of the ventral nerve cord reduced the frequency of the high-amplitude pulsations and abolished the ability of the abdominal heart to respond to thoracic heating.

6. When the heat was applied to the thorax, but not to the abdomen: (a) T_{Th} increased while T_{Ab} remained near T_A ; (b) T_{Ab} then increased while T_{Th} stabilized near 40-42 °C; (c) finally, if the heat input was not excessive, T_{Ab} also stabilized at a temperature above T_A .

7. Neither stabilization of T_{Th} nor increase of T_{Ab} were observed during thoracic heating of dead moths or those with transected nerve chords.

8. The distribution of temperature observed in the abdomen during thoracic heating is not explicable in terms of heating by conduction from the thorax.

9. During modest thoracic heating, decreases of T_{Th} were correlated with intervals during which there were full-length pulsations of the dorsal vessel. During periods where movement of the vessel was observed only at the anterior end of the abdomen, the temperature of the thorax increased.

10. Calculations of blood flow and heat flux indicate that the regulation of T_{T_h} in the observed range is physically reasonable by blood circulation alone.

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