Heartbeat Reversal and Its Coordination with Accessory Pulsatile Organs and Abdominal Movements in Lepidoptera

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Heartbeat Reversal and its Coordination with Accessory Pulsatile Organs and Abdominal Movements in Lepidoptera

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Summary. Haemolymph in certain Lepidoptera at rest is periodically transported from the anterior body to the abdomen and reversed by the coordinated activity of the heart, the accessory pulsatile organs and the abdomen. This oscillatory haemolymph transport is suggested to support haemolymph exchange and air ventilation in the anterior body and wings.

Although heartbeat reversal has been repeatedly described in insects[1-7], it is now generally regarded as being not essential for circulation, but rather a disturbance of heart automatism[6,8] or perhaps a stress reaction[5,9]. In some recent papers, which deal with the electrophysiology of heart rhythm in moths, reversal is either not mentioned[10,11] or is regarded as a rare and irregular event[12]. While mechanisms inducing and controlling heartbeat reversal were the central point of interest[2,5,6,13], little has been elaborated about its function[2,13,14].

Results. A new method, 'contact-thermography'[15] (Figure 1), allows one to examine free, resting insects during their whole lifetime without damage or narcotization, so that periodic heartbeat reversal could be shown to be a regular performance in pharate and adult moths (*Attacus atlas* L., *Argema mittrei* Guér., Saturniidae, Figure 1) and butterflies (*Caligo brasiliensis* Fldr., Brassolidae)[15]. Simultaneous recording of the heart, meso- and metathoracic pulsatile organs (PO's), which are responsible for the adduction of wing haemolymph[11,16] showed that these PO's pulsate intermittently with their activity periods mainly during backward beating and the pauses coincidental with forward beating of the heart (Figure 2). More precisely, an effective haemolymph convection by the PO's begins somewhat later than the backward periods and the pulsations extend into the heart's forward periods. Some time after the start of backward periods, peristaltic movements of the posterior abdominal part can generally be registered in all individuals, but they do not occur in every backward period (Figure 2). The beginning of the forward beating of the heart is generally accompanied by one slow abdominal contraction. The convective effect of this large contraction is perceptible even on the meso- and metascutellum. The haemolymph inflow in the anterior body thus happens much more vigorously than the evacuation. The presence of much more haemolymph in the anterior body during the forward periods is shown by the improved heat dissipation: despite the pauses in the PO's and constant haemolymph temperature, the equalized temperature level on the thorax remains below that of the backward periods.

Discussion. The question is, how the evacuation of the wings takes place when they contain an excess of haemolymph after expansion (8 times normal in *Bombyx*[17], 5 times in *Attacus*) and how an efficient exchange of haemolymph with that from the abdomen is guaranteed in species with relatively large wings. The generally accepted model of circulation in the wings with afferent and efferent sinuses, joined to a longitudinal body circulation[8,16,18], would imply a short circuit wing supply: the haemolymph once sucked out of the wings by the PO's must be taken to the head by the aorta. It leaves the frontal sac and enters the thoracic cavities, whence it can enter the anterior wing veins again, only a part of it being exchanged. The delay in the start of transport activity of the PO's seems to be a key for the understanding of heartbeat reversal and the mechanism of wing supply. As the head and thorax become drained shortly after backward peristalsis has begun, there must be a haemolymph deficiency when the PO's start their activity. Thus the anterior aorta and the lateral thoracic passages to the PO's[16] do not compete with those from the wings, so that haemolymph can be sucked mainly from the latter; additionally no haemolymph can be available to enter the wing veins during backward periods. The wings must also become drained. One function of the haemolymph oscillations, instead of a pure circulation, would be to accomplish an effective exchange in the wings containing relatively large amounts of haemolymph. The correlation of backward pulsations to the quantity of wing haemolymph becomes obvious in *Caligo*, where the duration of backward periods is increased after wing expansion[15]. The to and fro movements

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of blood cells observed in the wings, especially the pupal wings of *Ephestia*[19], show that similar conditions may exist in Microlepidoptera.

When the wing haemolymph becomes reduced after wing expansion, the soft cuticular surfaces can give way and approach one another, while the veins in fully developed adults are rather sclerotized. Changes in haemolymph pressure are thus presumed to be compensated by the large tracheae in the wing sinuses and by the airsacs of the thorax and head, which must expand by haemolymph evacuation during the backward periods.

The wing tracheae must contract under their own elasticity as soon as haemolymph flows in from the anterior body at the beginning of the forward period. The activity of the PO's on the one hand, and the elasticity of the tracheae on the other, would thus be antagonistic forces for air- and haemolymph ventilation in the wings, supported by coordinated directional changes of heart peristalsis and abdominal movements.

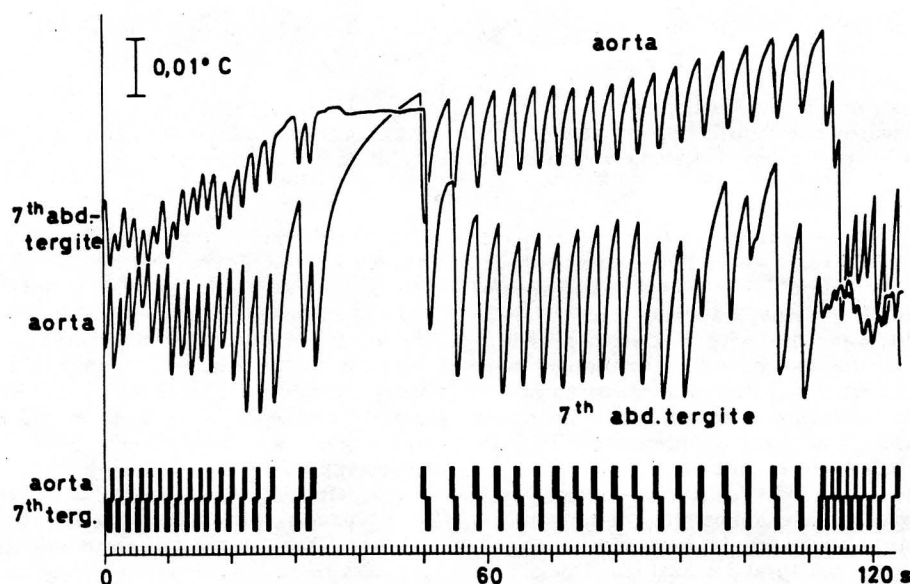[19] H. ZELLER, Z. Morph. Ökol. Tiere *34*, 663 (1938).

Fig. 1. Thermocardiograms of *Argema mittrei* (♂, 14 days old), representing the (convective) activity of the heart during forward and backward beating. Each thermogram is produced with one thermistor (diam. 0.1 to 0.25 mm), which at the same time serves for applying heat ($\Delta \vartheta +$ 1.8 °C) to the cuticle above the pulsatile organ and for the measurement of temperature differences: Each pulse removes the applied heat to an extent corresponding to its transport capacity. Each black bar represents the moment of convective cooling during heart contraction. In backward beating the contractions are first visible in the aorta.
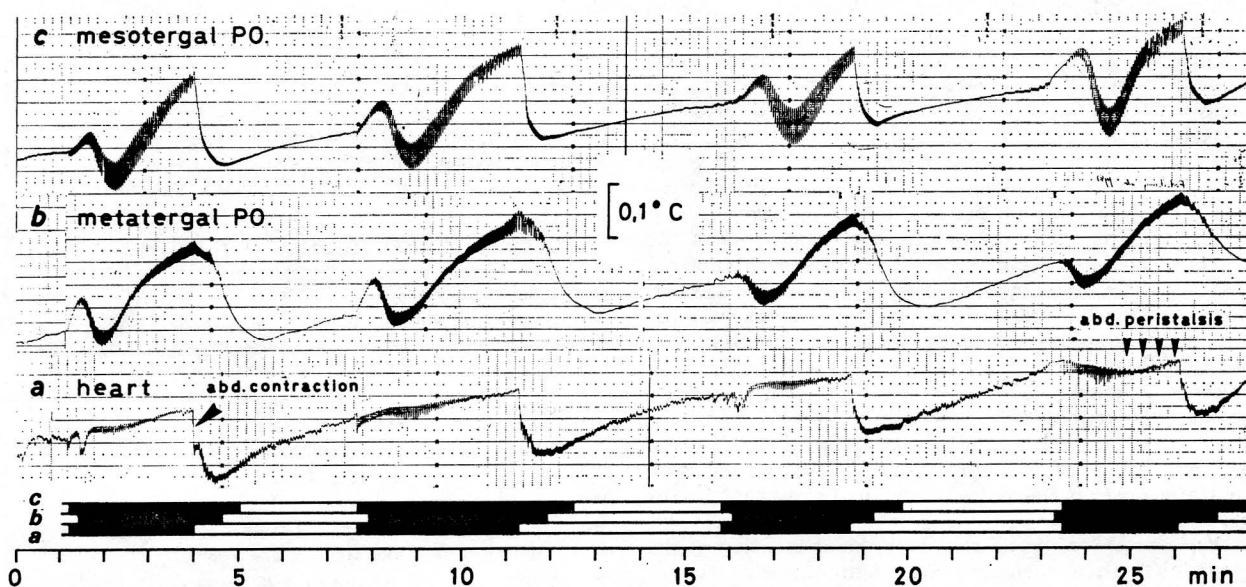

Fig. 2. Thermograms of *Attacus atlas* (♀, 2 days old), a) heart (2nd abdominal tergite), b) metatergal pulsatile organ (metascutellum), c) mesotergal pulsatile organ (mesoscutellum). The thermograms show the integrated convection beneath the measuring point. The pulses are superimposed on periodic slow waves of abdominal movements and alternations of heat dissipation, caused by (haemolymph-) mass changes. Black bands in a) backward periods, in b) and c) activity periods.