Central Nervous System Control of Circadian Rhythmicity in the Cockroach

III. The Optic Lobes, Locus of the Driving Oscillation?

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Summary. 1. We found no evidence that the thoracic ganglia which effect locomotory movements are themselves autonomously (circadian) rhythmic in their activity.

2. The abdominal ganglia play no role in effecting the rhythmicity of the thoracic ganglia, and hence, of locomotion.

3. We found positive evidence that the suboesophageal ganglion does not control the locomotory rhythm by a rhythmic secretion of a hormonal agent. It does, on the other hand, control activity level by a neural channel.

4. The evidence is strong that the driving oscillation is in the brain, in fact in the protocerebrum.

5. The pars intercerebralis suppresses (by a hormonal channel) the level of activity. It also, and separately, mediates locomotory activity by a hormonal channel.

6. The pars intercerebralis can however only cause rhythmicity of locomotion when it has intact neural connections with the optic lobes.

7. The driving oscillation in the nervous system responsible for the circadian rhythm of locomotory activity is thus — probably — localized in the optic lobes.

8. Animals in which the left optic tract and the right optic nerve have been severed display a freerunning rhythm in a 24 hour light/dark cycle: the driving oscillation in the left optic lobe is uncoupled from the pars intercerebralis which it therefore cannot drive; the oscillation in the right optic lobe can drive the pars intercerebralis but is uncoupled from the right compound eye.

Zusammenfassung. 1. Wir fanden keinen Anhaltspunkt dafür, daß die Thorakalganglien, die die lokomotorische Aktivität beeinflussen, eine eigene autonome (circadiane) Rhythmik ihrer Aktivität besitzen.

2. Die Abdominalganglien spielen keine Rolle bei der Beeinflussung der Rhythmik der Thorakalganglien — und damit der Lokomotion.

3. Wir konnten zeigen, daß das Suboesophagalganglion die Bewegungsrhythmik nicht durch rhythmische Sekretion eines hormonalen Stoffes steuert. Es kontrolliert dagegen die Stärke der Aktivität auf nervösem Wege.

4. Starke Anhaltspunkte sprechen dafür, daß der steuernde Oszillator im Gehirn liegt, und zwar im Protecerebrum.

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5. Die *Pars intercerebralis* erniedrigt (auf hormonalem Wege) die Aktivität. Sie bewirkt ebenfalls — getrennt davon — lokomotorische Aktivität auf hormonalem Wege.

6. Die *Pars intercerebralis* kann jedoch nur dann eine Bewegungsrhythmik bewirken, wenn die nervösen Verbindungen mit den optischen Lappen intakt sind.

7. Der für die circadiane Rhythmik der Bewegungsaktivität verantwortliche steuernde Oscillator im Nervensystem ist deshalb wahrscheinlich in den optischen Lappen lokalisiert.

8. Tiere, deren linke optische Bahnen und rechte optische Nerven durchtrennt waren, zeigen eine freilaufende Rhythmik im 24 Std-Licht-Dunkel-Zyklus: Der steuernde Oscillator im linken optischen Lappen ist von der *Pars intercerebralis* entkoppelt, und er kann sie deshalb nicht steuern; der Oscillator im rechten optischen Lappen kann zwar die *Pars intercerebralis* steuern, aber er ist vom rechten Komplexauge entkoppelt.

**Introduction**

The work reported here was prompted by the following questions:

1. What is the fuller meaning of our earlier demonstration (NISHIITSUTSUJI-UWO, PETROPOULOS and PITTEENDRIGH, 1967) that the *pars intercerebralis* is essential to the expression of circadian rhythmicity in the locomotion of cockroaches? 2. Does the driving oscillation responsible for the observed rhythm originate in that fraction of the protocerebrum? — or is the (certainly necessary) rhythmic output of the *pars intercerebralis* driven by an oscillation originating elsewhere? 3. Are the thoracic ganglia that immediately control locomotion themselves autonomously rhythmic? 4. What is the role of the suboesophageal ganglion?

Our experiments fall into two major groups: Group I is concerned with the ventral cords and their ganglia including the suboesophageal ganglion (SG) which HARKER (1956, 1960a, b) has concluded can autonomously sustain a circadian oscillation which is responsible for the rhythm of locomotion. The facts from our experiments are incompatible with her position. We find no evidence that SG is a rhythmic center and we find, more positively, that the ganglion cannot mediate rhythmicity by endocrine means.

Group II is concerned with the brain. Here we confirm our earlier conclusion that an endocrine output from the *pars intercerebralis* (PIC) mediates locomotory rhythmicity; but that region (the PIC) is evidently not itself autonomously rhythmic: rhythmicity of its output depends on intact neural connections with the optic lobes.

**Materials and Methods**

We have used newly emerged adult males of *Leucophaea maderae* for the bulk of our experiments. *Periplaneta americana* (fresh males also) was used only occasionally. Rearing methods and conditions, the nature of our recording techniques, and the principal surgical procedures we use have all been presented in the two previous papers of this series (NISHIITSUTSUJI-UWO and PITTEENDRIGH, 1967; and NISHIITSUTSUJI-UWO and PITTEENDRIGH, 1968).