THE METABOLIC EFFECTS OF THE CORPUS ALLATUM HORMONE IN THE MALE DESERT LOCUST

II. SPONTANEOUS LOCOMOTOR ACTIVITY

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INTRODUCTION

In a previous paper it was established that there was a considerable accumulation of chloroform-soluble fat in male desert locusts following allatectomy after adult emergence, while gonadectomy or wounding had no such effect (Odhiambo, 1966*d*). In another paper cytological observations indicated that glycogen deposits also increased greatly after allatectomy (Odhiambo, 1966*c*). Now, fat—and to a lesser extent, glycogen—form the main energy reserves in the desert locust (Weis-Fogh, 1952). Preliminary experiments have indicated that allatectomized locusts tend to be inactive (Odhiambo, 1965). The possibility therefore arises that the accumulation of fat and glycogen after allatectomy may be due to the metabolic consequences following from the absence of the corpus allatum hormone (CAH). This suggestion will be examined in the following pages.

MATERIALS AND METHODS

The objective was to measure the amount of 'spontaneous' locomotor activity of individual locusts, i.e. locomotor activity under uniform or controlled environmental conditions and without interaction with other locusts. Because the maturation phero-mone secreted by mature male locusts is important for the sexual maturation processes of young adults (Loher, 1960) and for the activation of their neurosecretory system (Highnam & Lusis, 1962; Highnam & Haskell, 1964), the experimental locusts could be isolated in the recording apparatus for only a limited period. In the periods inter-vening between recording sessions the locusts were maintained under crowded condi-tions in the experimental breeding cages. The optimum recording session was found to be 3 days.

The recording apparatus was, electronically, essentially that described by Brown & Unwin (1961), except that only one pen recorder was mounted.

The arena consisted of a rectangular Perspex box ($14\frac{1}{2} \times 7\frac{1}{2} \times 5$ cm.) with an open bottom, firmly fixed into a shallow layer of sand to provide a familiar foothold for the experimental locust. Holes (with a diameter of 3 cm.) were cut at either end of the box to accommodate the projecting housing for an infra-red light source and a photocell at the opposite ends; another similar hole was cut at the top of the box through which objects could be introduced into the arena. Wheat seedlings, bran, and water were freshly provided every morning, the whole operation taking only 10–15 sec. The entire

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arena was housed in a breeding cage maintained at $30 \pm 1°$ C. (Odhiambo, 1966a). A 40 W. fluorescent bulb provided light in the cage, which was completely masked by a thick black cloth.

The phototransistor was connected to a solenoid which operated a pen. Interruption of the infra-red light beam was recorded by the pen on the smoked paper. The motor and the wheels running the drum were geared and arranged so that the drum travelled about 28 cm. every hour and revolved once in every $3\frac{1}{2}$ hr. The line traced by the pen took a spiral course, so that a continuous 3-day record could be traced on a single smoked actograph paper.

Experimental locusts were taken from locusts which had previously been maintained under more or less continuous light conditions. The locusts were usually left to settle in the observation arena for $\frac{1}{2}$ hr. before recording began. Experiments were started at about 5 p.m., and left to run for 3 days continuously.

The surgical methods used have been described in a previous report (Odhiambo, 1966a).

<div align="center">RESULTS</div>

<div align="center">The problem of rhythm</div>

Since our main target was to find the effect of allatectomy on general muscular activity, we were interested in eliminating any possible complicating effects of circadian phenomena, such as those recorded by Harker (1960) in which sectioning of the allatal nerve to the suboesophageal ganglion leads to the gradual fading of circadian locomotor activity in the cockroach *Periplaneta americana*. Preliminary observations on the periodicity of locomotor activity in the desert locust were therefore carried out.

Light is the most important environmental factor regulating the timing of the phases of circadian rhythms in most animals (Harker, 1964). Evidence for circadian locomotor activity in mature male desert locusts was looked for by determining the amount of activity during various régimes of photoperiod. Experimental animals were bred under continuous light until required.

Under normal alternating periods of light and darkness (12 hr. each), there was a pronounced periodicity in spontaneous locomotor activity, with most activity taking place during the light period, and almost total quiescence during the dark period (Fig. 1a). The assumption of a periodicity in locomotor activity was 'instantaneous', i.e. the rhythm was assumed the same day the locusts were put in the activity arena after previously breeding the experimental animals under constant light conditions. This finding suggested that if the light/dark conditions were reversed soon after the experimental animals had undergone a 3-day period under a 'normal' photoperiod and assumed a 'normal' rhythm of activity, that they would instantaneously assume a new rhythm based on the onset of the new dark period. When this experiment was carried out, it was proved that this was indeed the case (Fig. 1b).

During a normal or 'reversed' rhythm of locomotor activity, the greatest amount of activity was during the light period while there is little movement during darkness. The crucial test in demonstrating a circadian rhythm is to show that under constant conditions the old rhythm persists for some time. Fig. 1c shows that under constant light conditions, after a normal or reversed light/dark régime, the previous rhythmic
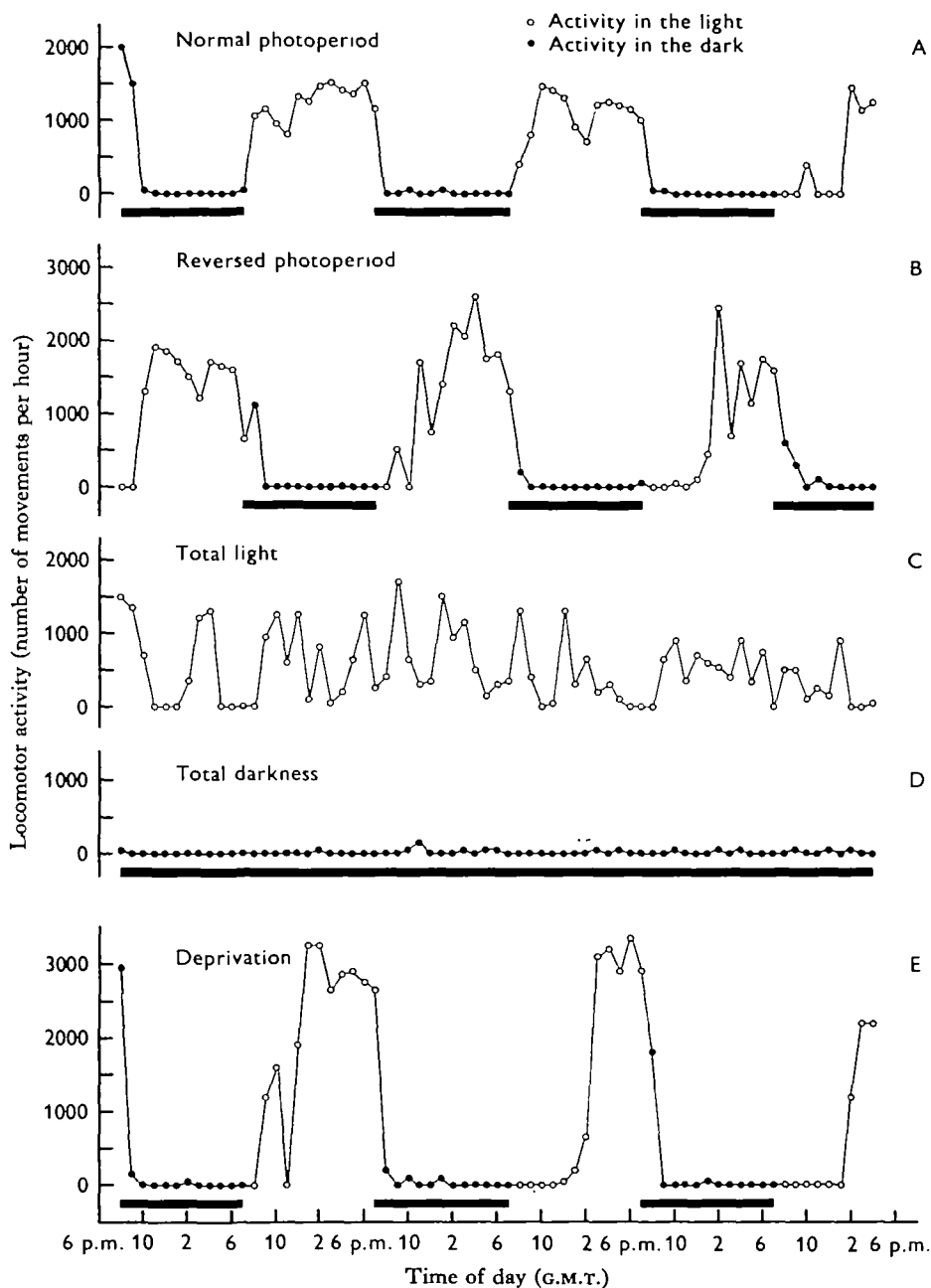
Fig. 1. Periodicity in the spontaneous locomotor activity of male adult locusts. Each record occupies 3 days. The heavy black lines at the bottom of the records indicate the time when the observation arena was in darkness. O, Activity in the light; ●, activity in the dark. A, activity under alternating light and dark periods of 12 hr. each, immediately after breeding the locusts in continuous light. B, activity under reversed light and dark periods, after the locusts have established a rhythm of locomotor activity under a normal photoperiod. C, activity in continuous light, after locusts have already established a rhythm of activity under a normal régime of alternating light and dark periods. D, similar locomotor activity in continuous darkness. E, activity of locusts denied food and water, but exposed to a normal light/dark photoperiod.

locomotor activity disappeared instantaneously. Similarly, under constant dark conditions the rhythm of activity again disappeared (Fig. 1*d*). The latter experiment, however, uncovered a further point; there was continuous, almost total, inactivity throughout the observation period of 3 days.

Animals which had been subjected to continuous light conditions were also introduced into an actograph with a normal light/dark photoperiod, but denied food and water for the 3-day observation period (male adult locusts die within 4–5 days as a result of such deprivation). As expected, there was an increase in the amount of locomotor activity; but the rhythms of activity resembled those already demonstrated for fed locusts in similar light/dark conditions (Fig. 1*e*).

Control of the intensity of activity

The experiments already reported appear to eliminate the occurrence of circadian rhythm in the locomotor activity of the male desert locusts. The experiments now to be described were designed to reveal the effect of allatectomy and other surgical procedures on the intensity of spontaneous locomotor activity of male locusts over a relatively long period of the adult life.
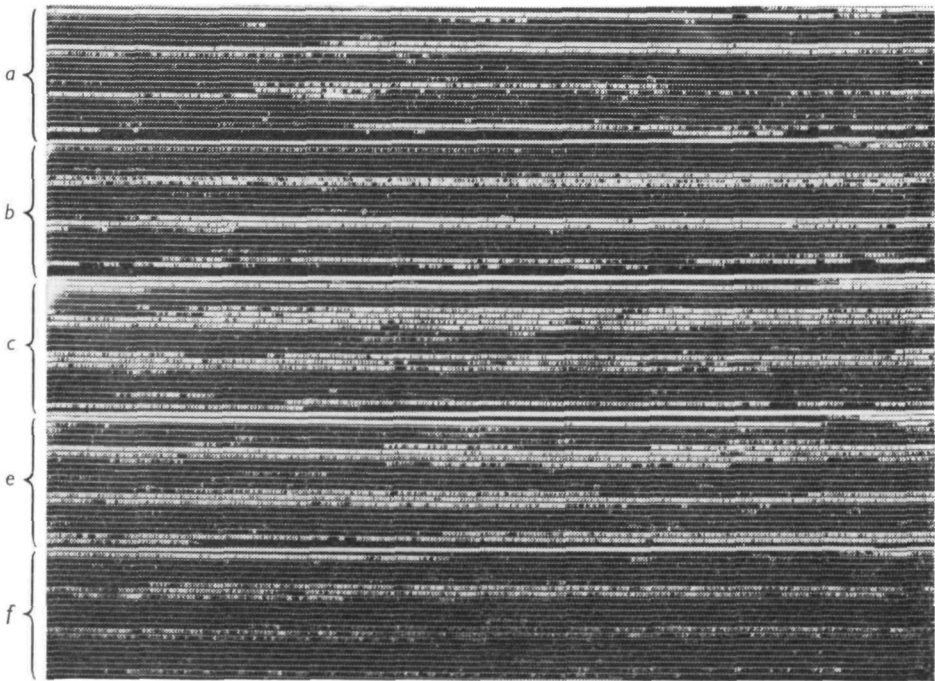

Fig. 2. Locomotor activity of unoperated locusts under a normal light/dark photoperiod (of 12 hr. each).

Notes for Figs. 2–8: (i) Each record lasts for 3 days, from 5 p.m. on the first day the experimental animal is introduced into the activity arena to about 5 p.m. on the fourth day. (ii) Usually, records are shown for each experimental treatment covering the period 4–25 days after adult emergence: *a*, starting from day 4 (immature); *b*, starting from day 7 (almost mature); *c*, starting from day 10 (fully mature); *d*, starting from day 13; *e*, starting from day 16; *f*, starting from day 22 (senescent).

Fig. 2 shows that the activity of an immature male adult locust is rather low, but by the time the locust is 7 days old it shows intense locomotor activity lasting about 7–9 hr. during the day. The intensity of this activity reaches a peak between 10 and 17 days after adult emergence, when the locusts exhibit about 10 hr. of almost continuous activity. The amount of locomotor activity is subsequently reduced, although still very high; and this high level of activity continues for the rest of adult life.
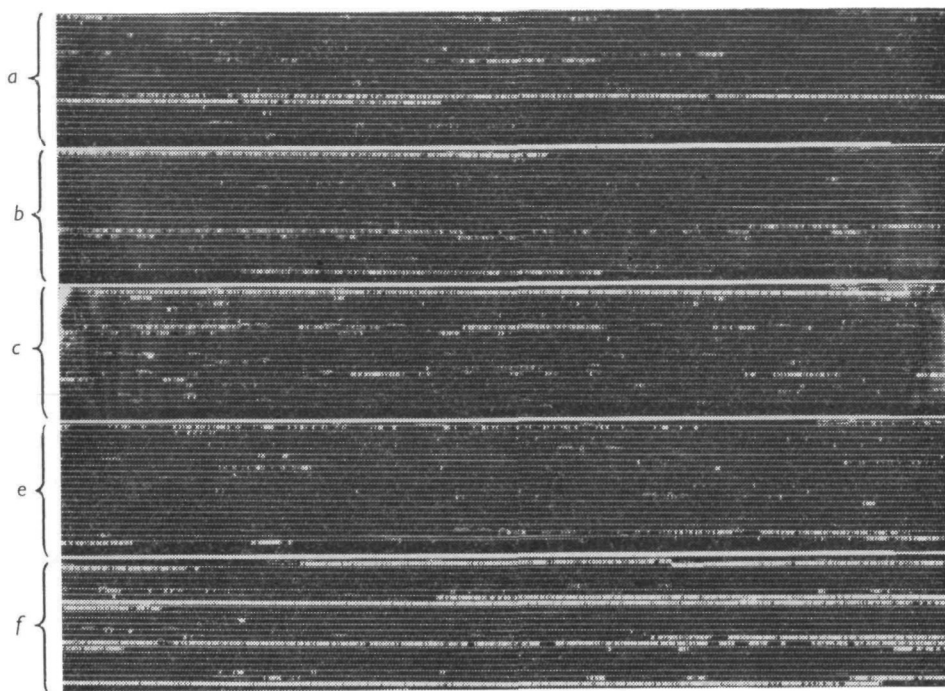

Fig. 3. Activity of male locusts allatectomized on the day of adult emergence.

It should be noted that male desert locusts, under the breeding conditions employed here, became sexually mature 6–10 days after adult emergence (Odhiambo, 1966a); and that the hormonal activity of the corpus allatum reaches a peak about this time and then declines somewhat as the male locust advances towards senescence (Odhiambo, 1966b). Thus, there seems to be a correlation between the concentration of the CAH in the haemolymph and the intensity of locomotor activity of the adult locust.

This suggestion was confirmed by allatectomy experiments. After allatectomy immediately following adult emergence, there was a persistent low level of activity (Fig. 3). At best, there were only 4–5 hr. of fairly intense activity at any time during adult life. In contrast, in sham-operated controls, the level of locomotor activity was extremely high throughout the major portion of the duration of observations, apart from the first 6 days of adult life when the insect was still sexually immature (Fig. 4). There is no doubt, therefore, that allatectomy has a profound effect on locomotor activity.

In earlier experiments on sexual maturation it was shown that maturation processes need the constant presence of active corpora allata for the state of maturation to be

maintained (Odhiambo, 1966 a). It was natural to test for a similar situation in regard to locomotor activity. Fully mature (7-day-old) male locusts were allatectomized, and their locomotor activity recorded for several days after that. There was a drastic
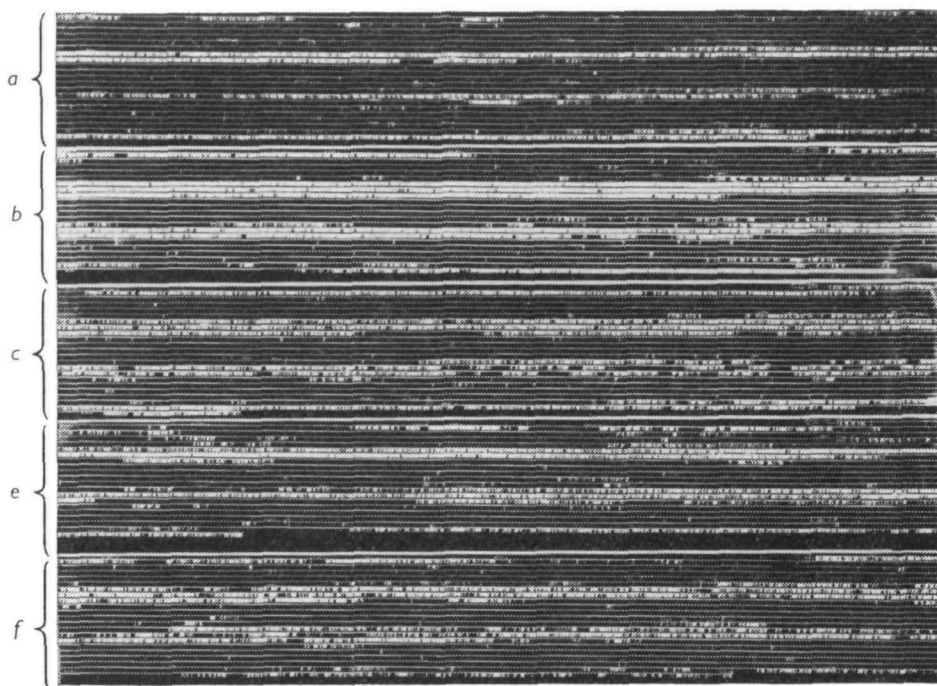

Fig. 4. Activity of sham-operated locusts, the operation having been performed on the day of adult emergence: a–c, sham operation for allatectomy; e and f, sham operation for gonadectomy.
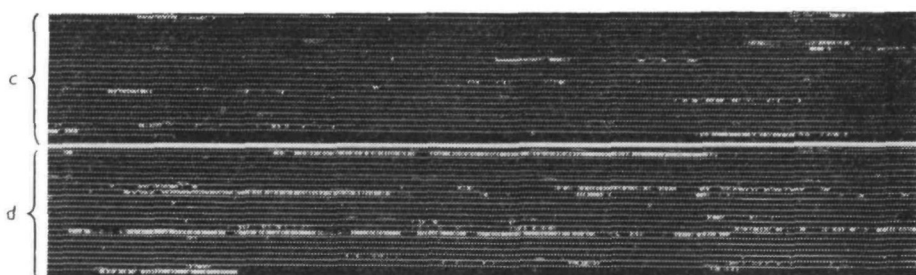

Fig. 5. Activity of adult locusts allatectomized when 7 days old.
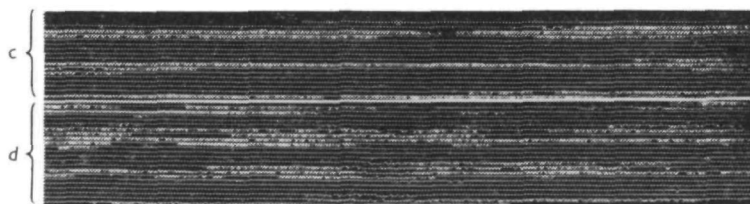

Fig. 6. Activity of adult locusts sham-operated when 7 days old.

reduction in the level of locomotor activity (Fig. 5) compared with that of sham-operated controls (Fig. 6).

The question arises whether the reduction in activity after allatectomy can be restored by implanting active corpora allata. The problem was investigated by allatectomizing newly emerged male locusts, and then implanting into the abdomen of each allatectomized locust two corpora allata from 12-day-old adult males. Previous bioassay of corpora allata of adult males of various ages had already established that those from adult locusts 10–15 days old were highly active (Odhiambo, 1966*b*).
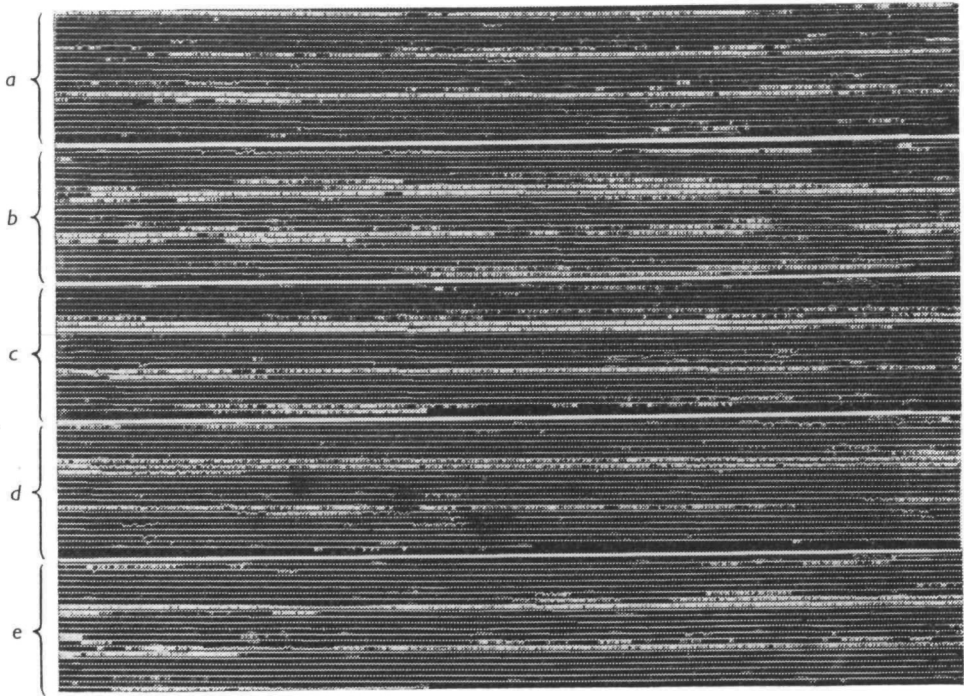

Fig. 7. Activity of locusts allatectomized soon after adult emergence, then immediately implanted with one pair of active corpora allata.

Locomotor activity of allatectomized locusts with implanted corpora allata was clearly very high (Fig. 7) as compared to that of allatectomized locusts (Fig. 2). It can thus be concluded that active corpora allata restore activity in allatectomized locusts to its normal level. In addition, it may be surmised that the control of the intensity of locomotor activity by the corpora allata is by way of a blood-borne factor.

Fingerman, Lago & Lowe (1958) maintain that in the grasshopper, *Romalea*, total locomotor activity remains unchanged after allatectomy. However, their observations were recorded one day after the operation, and for the duration of only a single day.

The male gonads do not seem to exercise any controlling influence on the level of activity of desert locusts. Extirpation of both testes and accessory reproductive glands soon after adult emergence did not lead to any significant change in the intensity of general activity (Fig. 8).

The vital fact that has been established with these experiments is that the CAH regulates, in some way, the intensity of locomotor activity in the male adult locust.
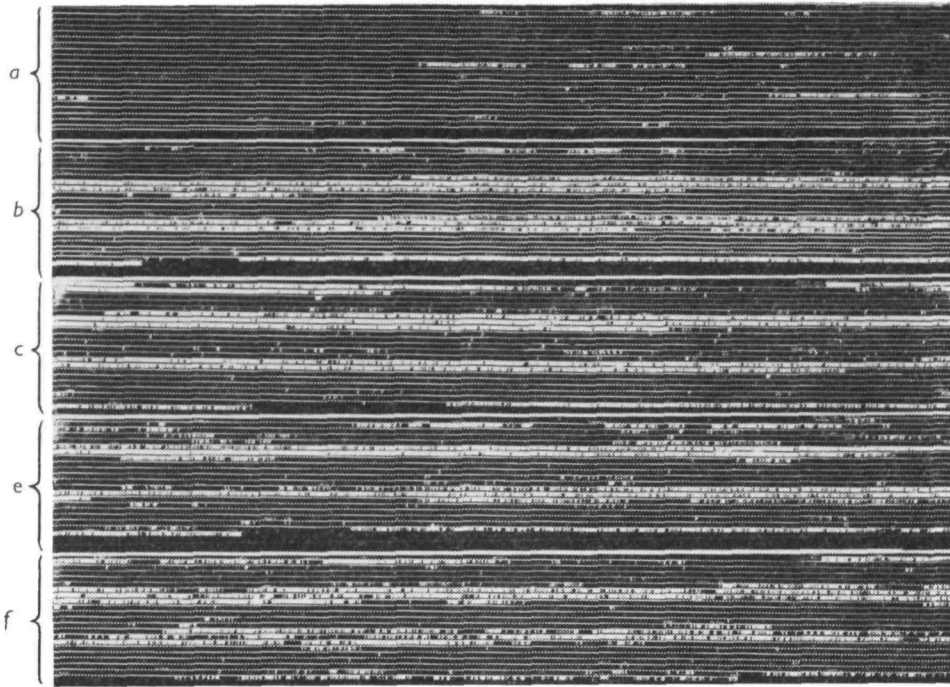
Fig. 8. Activity of locusts gonadectomized soon after adult emergence.

DISCUSSION

Fat body hypertrophy

In the course of extensive observations on the metabolism of the grasshopper *Melanoplus* in relation to its maturation, Pfeiffer (1945) established that (*a*) there was an early phase during which fatty acids (and also water and dry matter) were accumulated in the fat body and elsewhere; (*b*) during each cycle of oocyte development, there was a great increase of these materials; (*c*) coincident with the beginning of yolk deposition in the oocytes there was considerable depletion of the accumulated fat; (*d*) this depletion of accumulated reserves occurred equally well in ovariectomized adults; but (*e*) in allatectomized females there was continued accumulation of fat and the fat body hypertrophied greatly. Pfeiffer concluded from these observations that the corpus allatum acted by releasing a 'metabolic hormone' that in some way regulated the mobilization of precursor materials for the maturation of the oocytes. What she did not explain, however, was the continued depletion of fat after removing the supposed biochemical sink for these materials, namely the ovary.

Orr (1964*a*, *b*) has made similar detailed observations in various tissues and has estimated protein, carbohydrate, and fat during the maturation of the blow-fly *Phormia*. The following were the relevant findings: (*a*) the cycle of growth of the fat body in the female fly when ovariectomized was exactly the same as when it was sham-operated; (*b*) part of the reason (suggested from dissections) for the lack of fat-body hypertrophy in ovariectomized flies appeared to be due to their inability to digest food;

(c) allatecomy was followed by the hypertrophy of the fat body in both males and females, and combined allatectomy and ovariectomy did not affect this hypertrophy, except that during the first 3 adult days it occurred more slowly; and (d) fat-body hypertrophy was largely due to fat accumulation. From these results Orr postulated that the primary action of the CAH was upon the fat body, that it might regulate the enzyme system concerned in lipid metabolism in the fat body, and that its effects on vitellogenesis were secondary manifestations.

One vital assumption on which Orr's hypothesis is based is that ovariectomized flies do not digest their food at a normal rate. On that basis one could resolve the problem of the extra-ovarian utilization of lipid (and other) precursors that Pfeiffer's earlier experiments had suggested. Feeding experiments with adult male locusts show otherwise: neither gonadectomy nor allatectomy alters the pattern or intensity of feeding and the amount of digestive enzymes available (Odhiambo, 1966a). Consequently, in the desert locust, it is clear that feeding and digestion can be discounted as factors in the control of the metabolism of the fat body.

A fresh approach to the problem posed by Pfeiffer was begun when it was noticed that allatectomized locusts tended to be inactive (Odhiambo, 1965).

Detailed observations on the spontaneous locomotor activity of male adult locusts have clearly shown that the activity of an allatectomized locust is persistently extremely low. On the other hand, gonadectomy does not interfere with the high level of activity normally shown by adult locusts. That the level of locomotor activity is in some way controlled by the CAH was indicated by two additional experiments. In one experiment corpora allata were extirpated from already mature locusts showing the normal high level of locomotor activity; within 3 days, the level of locomotor activity was drastically reduced. In the other experiment, a high level of locomotor activity was restored by implanting active corpora allata into previously allatectomized locusts.

Now it has been shown both cytologically (Odhiambo, 1966c) and by extraction methods (Odhiambo, 1966d) that there is considerable accumulation of fat following allatectomy of male locusts soon after adult emergence. After gonadectomy, on the other hand, there is a progressive depletion of fat reserves during the period following the attainment of sexual maturity. Such depletion of fat reserves is normal in unoperated locusts. Implantation of active corpora allata reverses the tendency to fat accumulation. It is now clear that these changes in fat reserves are closely paralleled by the changes in locomotor activity.

Fat constitutes the chief energy reserve for the desert locust (Weis-Fogh, 1952; Kilby, 1963). For instance, during flight at least 80% of total energy requirements come from lipids (Weis-Fogh, 1952). It may be postulated that the accumulation of fat in allatectomized male locusts is due to their persistent inactivity.

There does not seem to be any need to invoke the existence of either a 'metabolic hormone' secreted by the corpus allatum (Pfeiffer, 1945), or an 'ovarian hormone' released by an active ovary (Doane, 1960, 1961)—both being supposed to regulate the mobilization of lipids and glycogen from the fat body. The extra-ovarian utilization of lipids, first demonstrated by Pfeiffer (1945), can now be explained as that portion of lipid stores used up during muscular activity.

Control of activity by the corpus allatum hormone

The suggestion mentioned above immediately raises the question of how the CAH may control muscular activity. It may be that the CAH regulates fat mobilization through its effect on the enzyme system in the fat body responsible for such mobilization (Orr, 1964b). But there is as yet no evidence for such a regulatory mechanism. Recent observations by Stegwee and his colleagues on the reversible degeneration of flight muscles in diapausing *Leptinotarsa* have suggested another explanation. Stegwee, Kimel, de Boer & Henstra (1963) demonstrated, by electron microscopy, that the flight muscles of diapausing *Leptinotarsa* were characterized by degenerated fibres and complete lysis of sarcosomes. At the end of diapause the flight muscles were fully regenerated and the sarcosomes appeared normal in structure. These authors showed that allatectomy has the same effect as diapause, and the re-implantation of active corpora allata has the same effect as the termination of diapause. Stegwee (1964) followed up these structural changes by showing that sarcosomes from diapausing beetles were inactive, while those from beetles one day after the termination of diapause had their respiratory functions fully restored. These experiments suggested the possibility that the CAH might control the sarcosomal respiratory system and the reversible degeneration and regeneration of flight muscles (Stegwee, 1964). Such a hypothesis seems to fit in well with the earlier work of Clarke & Baldwin (1960) on *in vitro* effects of the CAH on mitochondrial respiration. They found that the addition of corpora allata to mitochondrial preparations from fat body or thoracic muscles of adult *Locusta* resulted in an increase of oxygen consumption 8–20 % above the level in the control preparations. They suggested, therefore, that the CAH acted directly on the mitochondria, since the amount of hormonal stimulation of oxygen consumption in their experiments was of the same order of magnitude as was found in intact insects. However, this hypothesis does not supply an explanation for the observation that the addition of corpora allata to mitochondrial preparations from larval *Schistocerca* fat body inhibited oxygen consumption.

Electron microscopic study of the acessory reproductive glands, and their associated muscle layer and other tissues, has shown that allatectomy of the desert locust does not lead to the degeneration of mitochondria in any tissue at a level above that normally encountered (Odhiambo, unpublished observations). There was, in addition, no marked increase in the number of lysosomes. It should be noted that some recent studies on the degeneration of intersegmental muscles of the silkworm *Antheraea* point to other factors besides the CAH being concerned in the regulation of muscle degeneration in the adult insect. Lockshin & Williams (1964) found that intersegmental muscles broke down within 48 hr. of adult emergence, and their programming to do so seemed to be determined at the onset of adult development: thus, if CAH was injected before the initiation of adult development the breakdown of intersegmental muscles was prevented. However, the final signal for the process of degeneration to begin appeared to reside within the muscles themselves; when pupae were connected by parabiosis the disappearance of intersegmental muscles occurred independently in the two united animals—an observation which implied the absence of any humoral signal. Lockshin & Williams (1965a) have now shown that the intersegmental muscles are destroyed by the rupture of lysosomes; but the actual signal for muscle lysis is

provided by the cessation of efferent impulses from the nerves which supply the muscles concerned (Lockshin & Williams, 1965 b). It seems, from the evidence at hand, that the CAH control of muscular activity by the direct control of mitochondrial function is rather doubtful.

From experiments performed with adult desert locusts a working hypothesis may now be advanced: that the CAH regulates the level of locomotor activity by its direct effect on the central nervous system.

Three kinds of evidence seem to lend some support to this hypothesis. The first type of evidence comes from experiments on the regulation of sexual maturation. The initiation and maintenance of sexual maturation in the male locusts depends on the continuous supply of the CAH; it does not depend on the presence of any part of the gonadal system (Odhiambo, 1966 a). A fact of great interest is the observation that a sexually mature male tends to attack any moving object. This observation indicates that the regulatory neural mechanism responsible for sexual behaviour is in a highly excitable state in the mature male.

The second type of evidence comes from phototactic responses of certain insects, for instance in experiments using *Locusta* recently reported by Cassier (1963, 1964). Implantation of one or two pairs of corpora allata from a mature male into a male of the same age led to a greatly increased phototactic response and to increased speed of walking when the operated animals were tested 5 days later. The general increase in response had worn off 23 days after the operation, when histological observations showed both the implanted and host corpora allata to be inactive (Cassier, 1964). Both these sets of experiments indicate that increasing the level of the CAH results in increasing locomotor excitability of the central nervous system (or perhaps of the sensory receptors).

The third type of evidence comes from the apparent effects of the moulting hormone on the electrical activity of the central nervous system. During the electrical recording of the activity of the nervous system of the mature male *Schistocerca*, Haskell & Moorhouse (1963) found that a humoral factor from the late fifth-instar larva caused greatly increased electrical activity in the thoracic nerve cord and simultaneously a marked reduction of electrical activity in the motor nerves to the leg muscles. Ecdyson had similar effects. These results seemed to show that the reduced locomotor activity of late fifth-instar locust larvae and of isolated locusts was due to an increased titre of ecdyson. However, in crowded adult *Schistocerca* prothoracic glands disappear a few days after the last larval moult (Carlisle & Ellis, 1959); whereas allatectomy after a locust has attained sexual maturity (long after the prothoracic glands have disappeared) still leads to greatly reduced locomotor activity. Implantation of active corpora allata restores the normal level of locomotor activity. It is therefore clear that the CAH stimulates locomotor activity, possibly by increasing the excitability of the central nervous system. Since the prothoracic gland hormone is virtually lacking in the mature adult locust, it is not clear what part it plays in the control of locomotor activity—at least in the adult.

SUMMARY

1. An account is given of the pattern and intensity of the spontaneous locomotor activity of adult males of the desert locust. It is shown that desert locusts exhibit almost continuous activity under continuous light conditions, and almost continuous

inactivity in darkness. Under alternating light and dark conditions, the locusts assume a periodicity of activity which is not circadian since it may be 'instantaneously' changed by altering the light/dark régime.

2. Allatectomy of newly emerged adult locusts results in their persistent locomotor inactivity, which may be reversed by implanting active corpora allata. Allatectomy of sexually mature locusts similarly leads to inactivity. Gonadectomy has no such effect on locomotor activity.

3. The hypothesis is advanced that the corpus allatum hormone regulates the intensity of locomotor activity by its direct effect on the central nervous system. The accumulation of fat and glycogen after allatectomy may thus be explained as a consequence of the resulting lowered spontaneous locomotor activity since fat forms the chief energy reserves in the desert locust.

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