



Review

Circadian rhythms and endocrine functions in adult insects

Guy Bloch^{a,*}, Esther Hazan^a, Ada Rafaeli^b^a Department of Ecology, Evolution, and Behavior, The Alexander Silberman Institute of Life Sciences, Hebrew University of Jerusalem, Jerusalem, Israel^b Department of Food Quality & Safety, Agricultural Research Organization, Volcani Center, Bet Dagan, Israel

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ABSTRACT

Many behavioral and physiological processes in adult insects are influenced by both the endocrine and circadian systems, suggesting that these two key physiological systems interact. We reviewed the literature and found that experiments explicitly testing these interactions in adult insects have only been conducted for a few species. There is a shortage of measurements of hormone titers throughout the day under constant conditions even for the juvenile hormones (JHs) and ecdysteroids, the best studied insect hormones. Nevertheless, the available measurements of hormone titers coupled with indirect evidence for circadian modulation of hormone biosynthesis rate, and the expression of genes encoding proteins involved in hormone biosynthesis, binding or degradation are consistent with the hypothesis that the circulating levels of many insect hormones are influenced by the circadian system. Whole genome microarray studies suggest that the modulation of farnesol oxidase levels is important for the circadian regulation of JH biosynthesis in honey bees, mosquitoes, and fruit flies. Several studies have begun to address the functional significance of circadian oscillations in endocrine signaling. The best understood system is the circadian regulation of Pheromone Biosynthesis Activating Neuropeptide (PBAN) titers which is important for the temporal organization of sexual behavior in female moths. The evidence that the circadian and endocrine systems interact has important implications for studies of insect physiology and behavior. Additional studies on diverse species and physiological processes are needed for identifying basic principles underlying the interactions between the circadian and endocrine systems in insects.

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Abbreviations: AANAT, arylalkylamine N-acetyltransferase; Br, brain; CA, corpora allata; CC, corpora cardiaca; CNS, central nervous system; Clk, Clock a circadian clock gene; Crz, corazonin; Cry, Cryptochrome, a circadian clock gene; Cyc, Cycle, a circadian clock gene; DD, constant darkness; HIOMT, hydroxy-indole-O-methyltransferase; JH, juvenile hormone; JHBP, juvenile hormone binding proteins; LD, light-dark; OA, octopamine; PBAN, Pheromone Biosynthesis Activating Neuropeptide; Per, Period, a circadian clock gene; PG, prothoracic glands; PI, pars intercerebralis; PL, pars lateralis; SOG, suboesophageal ganglion.

* Corresponding author. Address: Department of Ecology, Evolution, and Behavior, The Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel. Tel.: +972 2 6584320; fax: +972 2 6584270.

E-mail address: bloch@vms.huji.ac.il (G. Bloch).

1. Introduction

The organization and operational principles of the endocrine system make it ideal for conveying temporal information from central pacemakers to tissues and cells throughout the body. Hormone production and release are regulated by the CNS which integrates information detected by the internal and external sensory systems. The hormonal signals circulating in the blood can reach each and every cell in the body. These basic characteristics enable clock-regulated endocrine signals to synchronize processes in cells that are not anatomically connected. Hormones are not only influenced by the central clock but may also modulate clock properties such as the phase or strength of circadian rhythms and can be involved in coupling oscillators that are not anatomically connected. In mammals and other vertebrates the circadian system influences the circulating levels of essentially all endocrine signals, and the functional significance of these oscillations has been explored (reviewed in Kriegsfield et al., 2002). The interplay between the circadian and endocrine systems is less explored in insects. In this review we focus on adult (imago) insects and the better characterized endocrine signals such as juvenile hormones (JHs), ecdysteroids, Pheromone Biosynthesis Activating Neuropeptide (PBAN), and melatonin. Further details including studies on the interplay between the circadian and endocrine systems during pre-adult development can be found in detailed reviews by Vafopoulou and Steel (2005), and Steel and Vafopoulou (2006).

1.1. The circadian system of adult insects

Circadian rhythms are defined as biological rhythms that meet the following three criteria: (1) they persist, or “**free-run**”, with a period of about 24 h in the absence of external time cues, (2) they are reset, or **entrained**, by environmental cues, in particular by light and temperature, and (3) they have a stable period length in a wide range of physiologically relevant temperatures. This phenomenon, commonly termed “**temperature compensation**”, is thought to require specific mechanisms because most biological reactions are accelerated when the temperature is elevated. The circadian system influences many physiological and behavioral processes in insects. These include activity, sleep-wake cycles, feeding, mating, oviposition, egg hatching, and pupal eclosion. The circadian system is also involved in measuring day length, and influences photoperiodism and annual rhythms such as diapause and seasonal reproduction (Dunlap et al., 2004; Saunders, 2002).

The circadian system has been traditionally described as having three functional components. The core pacemaker is a functional entity capable of generating endogenous rhythms with approximately a 24-h period. The central pacemaker is entrained by input pathways in which environmental signals are detected, converted to sensory information, and transmitted to the central pacemaker. Output pathways carry circadian information from the core pacemaker to various biochemical, physiological, and behavioral processes (Bell-Pedersen et al., 2005; Dunlap et al., 2004). These three functional entities can be found in a single cell or at higher levels of organization (e.g., a circadian network, see below). Endocrine signals can be involved in functions such as conveying circadian information to cells in tissues that do not have direct contact with cells of the circadian system, or coupling the activity of oscillators in different tissues. Cellular oscillators express a set of “clock genes” that interact in the form of interlocked autoregulatory transcriptional/translational feedback loops with positive and negative elements (Dunlap, 1999). Pacemaker cells in the brain and other tissues are interconnected in a circadian network that couples their activities and orchestrates normal rhythms in physiology and

behavior (Bell-Pedersen et al., 2005; Dunlap et al., 2004). It is currently acknowledged, however, that the circadian system is much more complex than this simplified framework. For example, the same genes and pathways are involved in both input and output functions (Zhang and Kay, 2010).

The molecular clockwork in oscillator cells consists of multiple interacting feedback loops (Zhang and Kay, 2010). At the organism level, the proper expression of circadian rhythms requires complex interactions between central and peripheral clocks (Dunlap et al., 2004; Bell-Pedersen et al., 2005). Genome-wide expression analyses suggest that the circadian clock influences many metabolic processes in insects, as well as in other animals (for example, fruit flies (Keegan et al., 2007; Xu et al., 2011), mosquitoes (Rund et al., 2011), and honey bees (Rodriguez-Zas et al., 2012)). The recent findings that metabolites such as heme and NAD⁺ also regulate the clock suggest that there are additional feedback loops in which chemical products of clock-regulated metabolic processes feed back to influence the circadian clockwork (Zhang and Kay, 2010). Post-translational regulation of clock proteins is also important, if not sufficient for molecular clock function and accurate timing of circadian transcription (Weber et al., 2011). Moreover, recent studies have revealed an evolutionary conserved ~24-h circadian clock that generates rhythms in the absence of transcription (including in red blood cells that do not have a nucleus; O'Neill and Reddy, 2011; Edgar et al., 2012). In this clock peroxiredoxins oscillate between reduced and oxidized forms in a circadian pattern. These post-translational rhythms showed hallmark features of circadian oscillators, including temperature compensation. This means that they maintained an approximately constant period-length of about 24 h over a physiological temperature range, and the oscillations could be entrained by temperature cycles. Recent studies further suggest that in animals, these metabolic cycles interact with the transcription-translation feedback loops of the clockwork (Edgar et al., 2012).

The insect for which the molecular and neuronal bases of the circadian clockwork has been best characterized is the fruit fly *Drosophila melanogaster* (see: Peschel and Helfrich-Forster (2011) for a recent review, and Zhang and Kay (2010) for an updated list of clock genes). The positive elements *Clock* (*Clk*) and *Cycle* (*Cyc*) form a dimer and activate the transcription of the negative elements, the transcription factors *Period* (*Per*) and *Timeless* (*Tim1*). *Per* and *Tim1* are translated into proteins that enter the nucleus where they interfere with the transcriptional activity of the CLK:CYC complex, and thereby shut down their own expression. *Par Domain Protein 1* (*Pdp1*), *Vrille* (*Vri*), and *Clockwork Orange* (*Cwo*) act together with *Clk* in an interlocked feedback loop that is thought to stabilize the *Per/Tim1* loop. Several additional proteins fine tune this cell-autonomous rhythm generation machinery by posttranslational modifications that affect the stability of the canonical clock genes. These include the kinases *Double-time* (*Dbt*), *Shaggy* (*Sgg*), *Casein Kinase II* (*CKII*), the *Protein Phosphatase 2A* (*PP2A*), and the F-Box protein *Slimb*. *Drosophila*-type *Cryptochrome* (*Cry-d*, also known as *insect Cry1*) has a photic input function. The neuropeptide Pigment Dispersing Factor (PDF) is involved in coupling oscillators and in output pathways in *Drosophila*. Recent genomics and functional genomic analyses have revealed notable variation in the set of clock genes encoded by the genomes of different insect species. Nevertheless, the basic organization principles of the molecular clockwork in insects appear to be conserved (Rubin et al., 2006; Zhan et al., 2011).

There is also much variation in the anatomical organization of the circadian network in the insect brain (Helfrich-Forster et al., 1998; Saunders, 2002; Sehadova et al., 2003; Závodská et al., 2003). Transgenic manipulations and immunocytochemical analyses have been used to characterize the anatomy and function of the brain circadian network of the fruit fly. The *Drosophila* clock net-

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