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“Neuroethoendocrinology”: Integration of field and laboratory studies in insect neuroendocrinology

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Abstract

Progress in the field of insect neuroendocrinology has been rapid despite the relatively small number of investigators working on insect systems. This progress, in part, reflects the ease of studying insect behavior in the laboratory, and a historical perspective reveals that insect neuroendocrinology has been dominated since its inception by laboratory studies. Recent advances in methodology and a renewed interest in the concept of behavioral state in insects suggest that it might be useful for insect neuroendocrinologists to spend a little more time in the field.

Keywords: Neuroethoendocrinology; Insect behavior; Octopamine

Introduction

Neuroethology is the biological discipline that seeks to understand the neural bases of naturally occurring animal behavior. We feel, as do many others, that neuroethology encompasses not only electrophysiological analyses of behaviorally-relevant neural circuits, but also includes the study of hormones and neuromodulators that organize and activate neural circuits. Analysis of activity in neuronal pathways defines behavior on time scales of seconds and minutes, whereas analysis of the neuroendocrine modulation of these pathways addresses issues about the matching of behavior to physiological state and the environment, often over time scales of hours to days. The present review describes traditional and contemporary approaches to the study of hormonal regulation of behavior in insects. Such studies have their origin in investigations of the endocrinology of insect molting, a behavior common to all of the 700,000+ species of insects alive today (Hoy, 2003). Most research in insect neuroendocrinology, however, has focused on behaviors of a few select groups, with no studies at all reported for many of the 29 orders of insects. The extraordinary biodiversity of insects suggests that numerous opportunities for the profitable application of August Krogh’s principle (“For many problems there is an animal in which it can be most conveniently studied”) are currently untapped.

One advantage of using insects to address questions in behavioral neuroendocrinology is that the experimental subjects often do not even notice that they have swapped the field for the confines of the laboratory! While this may reflect insensitivity on the part of human observers to nuances of invertebrate behavior, there is no doubt that it is easier to bridge the field–lab divide in insects than with many vertebrate taxa. Disadvantages of studying the behavioral neuroendocrinology of insects include the lack of commercially available reagents for study of insect hormones and the need to miniaturize commonly used assays. For example, radioimmunoassays have been developed that permit the measurement of circulating hormones

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in insect blood, but species such as the honey bee have a total blood volume measured in microliters, and taking a single blood sample from a bee is a terminal procedure (Huang and Robinson, 1995). The reduced size of brain interneurons in smaller insects poses a challenge for electrophysiologists, resulting in a situation where more is often known about the titers of hormones associated with a behavior than is known about patterns of electrical activity in the underlying neural substrates. And as is the case with many vertebrates, seasonal patterns of activity are characteristic of temperate-zone insects. This challenge has been met by devising methods for year-round laboratory rearing of several frequently used species of insects, including the tobacco hornworm *Manduca sexta*, the cricket *Acheta domesticus*, the honey bee *Apis mellifera*, and the fruit fly *Drosophila melanogaster*.

One striking difference between the vertebrate and insect neuroendocrine literature is a relative paucity of studies on the neuroendocrine control of reproductive behavior in insects. We are confident that this does not indicate the absence of such regulation, but rather the lack of ready parallels to vertebrates, beginning with fundamental differences in mechanisms of sex determination (Hoy, 2003). There are also relatively few examples of parental behavior in insects. A comprehensive review of hormonal signaling mechanisms governing insect reproduction has recently been published (Simonet et al., 2004), and this topic will not be discussed further here.

Our survey of the field focuses first on a “traditional” topic in insect endocrinology, the study of behaviors associated with molting. We show that our present knowledge base could be extended by a new wave of field studies. We next report recent research on the regulation of insect behavioral state by biogenic amines, particularly octopamine, in the context of the history of such investigations. The former topic is offered in the spirit of providing molecular biologists with an excuse to leave the lab every now and then in favor of the great outdoors; the latter topic is important because octopamine regulation often links insect behaviors rarely considered to be related. Viewing different behaviors (for example, aggression and foraging) through the lens of octopamine promotes the search for points of convergence in underlying neural circuits.

The primary literature of insect behavioral neuroendocrinology and endocrine neuroethology is scattered over numerous entomological and neurobiological journals, including the *Journal of Insect Physiology*, *Journal of Comparative Physiology A*, *Journal of Neurobiology*, *Advances in Insect Physiology*, and, notably, *Hormones and Behavior*. For students, insect examples are allocated a chapter in one major textbook of behavioral neuroendocrinology (Truman, 2002), mentioned occasionally throughout the text in another (Nelson, 2000), and ignored in a third (Pfaff et al., 2004) aimed at medical students. A monograph by Nijhout (1994) provides a concise introduction to insect endocrinology and includes a chapter on behavior. Broad coverage of hormone–brain–behavior relationships in insects is provided in two major, multi-volume reference works: *Hormones, Brain and Behavior* (Pfaff, 2002) and *Comprehensive Insect Molecular Science* (Gilbert et al., 2005). Historical perspective and coverage of the literature through the mid-1980s is found in the reference work *Comprehensive Insect Physiology, Biochemistry, and Pharmacology* (Kerkut and Gilbert, 1985).

Another valuable source of information on insect behavior derives from the long-established practice of beekeeping. Honey bees, living in hives provided by humans, interact freely with their environment and undergo a normal pattern of behavioral development (Robinson, 1992). This combination of living in field colonies, yet being as accessible as if they were laboratory-housed, provides unusual opportunities for neuroethoendocrinologists to explore the neural, endocrine, and genetic bases of complex social behaviors. Technical journals devoted to apiculture such as *Bee World*, *American Bee Journal*, and *Bee Culture* represent a distinctive, non-academic source of information on honey bee behavior that supplements the academic research literature.

Neuroendocrine control of behaviors associated with molting in insects

The recent discovery of a 505 million-year-old arthropod fossilized in the act of shedding its cuticle demonstrates that molting is an extremely ancient animal behavior (Garcia-Bellido and Collins, 2004). The development of silkworm rearing (sericulture) in China more than 6000 years ago implies early understanding of the life cycle of the silk moth (*Bombyx mori*), and even older paintings on plaster walls in Anatolia dated to 7000 BCE depict the life cycle of the honey bee (*A. mellifera*) in comb (Crane, 1999). However, it was not until the early 20th century that the experiments of the Polish scientist Stefan Kopec on the regulation of molting and metamorphosis in the gypsy moth inaugurated the field of insect behavioral neuroendocrinology (Kopec, 1922). Kopec’s studies set the tone for the subsequent development of the field by employing the classical neuroendocrine techniques of ablation and replacement to show that the brain was the source of a hormone that regulated molting. Kopec’s experiments neatly coupled the laboratory and the field, as he observed the effects of his manipulations on the naturally occurring behavior of wild-caught gypsy moths. Other early investigators of insect molting and metamorphosis were Wigglesworth, who studied the assassin bug, *Rhodnius prolixus*; Fraenkel, who studied the blowflies, *Calliphora* and *Sarcophaga*; and Fukuda, who studied the commercial silk moth, *B. mori* (Fraenkel, 1935; Wigglesworth, 1934). These investigators extended the work of Kopec by identifying additional glands and glandular “factors” that regulate postembryonic development in insects. This set the stage for the subsequent