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# Editorial overview: Neuroscience: How nervous systems generate behavior: lessons from insects

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Yehuda Ben-Shahar received his B.Sc. degree in Life Sciences from Tel-Aviv University, Israel in 1996 and a Ph.D. in Entomology from the University of Illinois, Urbana-Champaign in 2002. He is currently an Associate Professor of Biology at Washington University in St. Louis, USA. His research focus is on the genetic and neuronal processes that drive specific behaviors in insects. Current projects in his group emphasize the genetic and neuronal networks that support social interactions between conspecifics by using members of the *Drosophila* species group and bees as models. He is also very interested in the molecular evolution of insect genomes, and the role it plays in the emergence of novel complex behavioral phenotypes.

The bulk of the current insect neurobiological research enterprise is focused on a single insect species, the fruit fly *Drosophila melanogaster*. However, the scientific history of using diverse insect species for neurobiological studies is old and rich [1,2]. Accordingly, the diversity of unique behavioral adaptations offered by insects has served as an excellent model for studies of neuronal functions in the context of comparative ethology and the evolution of behavior. In this issue, eight reviews describe diverse and timely facets of modern insect neurobiology, which provide novel insights into their complex and intriguing behaviors.

How insects adapted their locomotion patterns to their specific ecological needs is a longstanding problem in comparative neurobiology. In their review, Amir Ayali *et al*. compare and contrast the locomotion patterns of two phylogenetically related orthopteroid insect species, the American cockroach *Periplaneta americana* and the stick insect *Carausius morosus*. Using evidence from experimental and computational approaches, they discuss the mechanistic tradeoffs between the typical flat surface running in the cockroach in contrast to the slow and precise leg placement observed in stick insects. Consequently, Ayali *et al*. demonstrate the value of comparative neurobiological approaches to fundamental problems in animal locomotion.

Like most other animals, insects show robust circadian rhythms. In fact, the fundamental genetic and molecular components of circadian biological clocks in animals were first described in the fruit fly, which is beautifully narrated in the book 'Time, love, memory: a great biologist and his quest for the origins of behavior' [3]. The discovery of similar mechanisms in mammalian cells initially suggested that insects and mammals have evolved somewhat different ways to tell time.

However, with the advances of molecular and genetic techniques in other insects, we now know that the clock mechanism in *Drosophila* is not conserved across the insect phylogeny.

Moreover, different insect lineages seem to have evolved somewhat different molecular variants of the general clock theme, some of which are much closer to the mammalian version than to the one found in the fruit fly. Here, Monika Stengl and Achim Werckenthin discuss the Madeira cockroach *Rhyparobia maderae* as a model for studies of a non-dipteran circadian clock. By taking advantage of its relatively large brain, and its amenability for lesion and *in vivo* electrophysiological studies, Stengl and Werckenthin describe with great details the contribution of this powerful model to the understanding of the relationship between neurocircuits, modulators, and behavior.

The recent advances in understanding the functional organization of the insect brain in diverse insects, in combination with the rapid advances in the development of genetic tools that enable the manipulation of specific neuronal circuits in the Drosophila brain indicate that in spite of its size, the insect brain shows a remarkable complexity that rivals the vertebrate brain. Two reviews in this issue are focused on specific high-function areas in the insect brain, and how studying them has provided important insights into how insects interact with their environment to generate adaptive behaviors. Sarah Farris and Joseph Van Dyke discuss the current state of research on the neuroanatomy and function of the 'mushroom bodies', a brain region that plays an essential role in the integration of sensory input from diverse modalities. By using the mushroom bodies as a model, Farris and Van Dyke demonstrate how the combination of functional studies in the genetically tractable *Drosophila* model system and comparative neuroanatomical studies in other insects has been a beneficial approach for deciphering the general principles that drive and support behavior in insects. Another very important and highly conserved region of the insect brain is the central complex, which is discussed by Jenny Plath and Andrew Barron. In contrast to the mushroom bodies, which are best understood in the context of processing of chemosensory information, the central complex seems to be responsible for integrating information that is important for behavioral decisions associated with locomotion and spatial navigation. As in Farris and Van Dyke, Plath and Barron argue that truly understanding the fundamental role of the central complex in insect behavior will require a comparative approach that takes advantage of the rich behavioral and ecological diversity of insects.

Insects also evolved diverse and very sophisticated sensory capabilities that allow them to perceive and react to their ever-changing environments in an adaptive manner. In this issue, three articles examine the interactions of insects with specific sensory stimuli. The review by Debajit Saha and Barani Raman examines the role of early processing of olfactory stimuli in behavioral decision making. By using recent and classic examples from studies in diverse insect species such as the locust *Schistocerca gregaria*, the tobacco hornworm moth *Manduca sexta*, and the fruit fly *Drosophila melanogaster*, Saha and Raman show that many of the innate and learned aspects of the response of individual animals to olfactory stimuli are processed early in the insect nervous system at the level of the olfactory sensory neurons and first order interneurons in the antennal lobe. By using experimental and computational information from diverse insect model systems, they demonstrate that peripheral processing of olfactory information is essential for chemosensory-driven behaviors. Another important aspect of insect chemosensation is the perception and processing of pheromones, which conveys information about their social environment. Ross McKinney *et al.*, discuss recent advances in understanding the how pheromonal signals are sensed and processed by the insect nervous system. In contrast to most other sensory systems, pheromones and their receptors are fast evolving to support species-specific functions. In their article, McKinney, Vernier, and Ben-Shahar review the current state of research in both the synthesis of cuticular pheromones in insects, and their perception by the nervous system. In addition, they review recent exciting findings about the higher neuronal circuits responsible for the processing of pheromonal information in the brain of Drosophila. While it is too early to determine how conserved the processing of pheromone information is in other insect species, these advances suggest that pheromone-driven behaviors are driven by dedicated neuronal circuits in a sex-specific manner.

Vision is another important sensory modality for many different insect species. One of the best examples of an extensive use of visual stimuli for identifying food sources and spatial navigation comes from studies of foraging behavior in bees. In their review, Natalie Hempel de Ibarra *et al*. discuss the role of chromatic and achromatic visual cues in guiding foraging honey bees in their quest to find and utilize floral resources. By using experimental data, the authors argue that honey bees perceive chromatic and achromatic cues via independent input pathways, which require higher level integration. Furthermore, they discuss the complexity of visual stimuli offered by flowers, and how bees have evolved specialized visual cognitive abilities to guide their use of the visual patterns of flowers while foraging.

While much of this issue has been dedicated to the integration of sensory information, the behavior of individual insects is also driven by their internal neuroendocrine state. Much of what we know about the function of 'juvenile hormone' (JH), as suggested by its name, comes from studies of insect development. In numerous studies, the coordination of neuroendocrine signaling by JH and ecdysone, the other classic insect hormone, regulates the pre-adult developmental transitions in many different insect species. However, studies in the honey bee and other social insects indicated that JH also plays an important role in regulating adult behavior. Here, Atul Pandey and Guy Bloch discuss JH as an insect behavioral modulator. By using evidence from behavioral, physiological, neuroanatomical, and genomic studies, they illustrate the importance of the regulation of brain gene expression via the interaction between JH and ecdysone signaling, which are associated with socially-regulated behavioral states in eusocial honey bees and bumblebees.

Covering all aspects of insect neurobiology is an impossible task. Consequently, the selection of articles that were chosen to be included in this issue of Current Opinion in Insect Science represents an extremely narrow facet of the historical and current state of insect neuroscience research. Nevertheless, my goal as the editor of this issue was to promote the value and importance of comparative approaches to studies of behavior and neurobiology in general, and of insects in particular. Like all other biological systems, nervous systems are amenable to evolutionary forces. Therefore, understanding behavioral adaptations in diverse model animals is key for recognizing the general principles that govern behavior. It is my hope that the comparative approach to fundamental insect neurobiological functions, broadly sampled in this issue, will entice others to integrate the power of comparative approaches into their favorite systems.

## References

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