C. Giovanni Galizia
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Honeybee Neurobiology and Behavior

A Tribute to Randolf Menzel

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THE NEUROBIOLOGY AND
BEHAVIOR OF HONEYBEES

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Prologue

Twenty-five years ago, Randolf Menzel and Alison Mercer edited a book that marked several generations of researchers and students who had chosen, for different reasons, the honey bee as a model for their studies. The book, whose title was Neurobiology and Behavior of Honeybees, was published in 1987, at a time in which studies on honeybee sensory physiology and learning and memory – which occupied an important place in the book contents – were intensively developed. Some of us used to read this book as students, attracted by its content and scientific contributions, but more than that, marveled by the apparently inexhaustible potential of the honey bee as a model to understand basic questions in biology. In a sense, the book was the best demonstration that Karl von Frisch (1886–1982), the father of studies on the behavior of honeybees, was right when he described honeybees as a "magic well" for discoveries in biology because "the more is drawn from it, the more is to draw".

In these last two decades, researchers have continued to draw from this magic well. We have seen the adoption of new ideas and concepts in the study of bee behavior and neurobiology, we have benefited from new tools for the analyses of the bee brain that were unimaginable some 20 years ago, and we have opened new research pathways with the advent of the genomic era, which resulted in the sequencing of the entire honeybee genome. Thus, to the question of "why producing a new version of the book Neurobiology and Behavior of Honeybees in 2011?" it seemed to us that the answer could be multiple.

We wanted to underline the potential of the honey bee as a model system to tackle different fundamental scientific questions, particularly at the behavioral, neural and molecular levels. In that sense, appreciating how research has evolved in the last two decades is important to appreciate where research is heading and which are the essential questions that we need to answer in the immediate and not so immediate future. At the behavioral level, for instance, fundamental changes have occurred since the 1990s mostly based on a conceptual switch that changed the way honey bee researchers view their study object. Despite the fact that the bee, like many other invertebrates, was traditionally a powerful model for the study of learning and memory, the questions and behavioral analyses that had been undertaken were concerned by simple associative learning forms, usually the establishment of a simple link between a visual stimulus or an odorant and sucrose reward. Yet, understanding the behavioral plasticity of an organism implies acknowledging that such elemental links are just part of its plastic repertoire and that higher-order learning forms, not amenable to simple associative analyses underlie sometimes problem resolution in a natural context. This conceptual twist adopted by several bee researchers in the last two decades has made of the honey bee one of the most tractable models for the study of cognitive performances. Indeed, studies on categorization, rule extraction, transitivity, top-down modulation of perception, and numerosity (to cite just some examples) have been performed in the honey bee, which are still out of reach in other powerful invertebrate models which despite disposing of fantastic tools for neuronal control do not exhibit the behavioral richness expressed by bees in these recent studies. Studies on navigation benefited from novel radar tracking technologies that allowed, for the first time, reconstructing entire flight pathways in the field, and thereby yielding the view that bees build spatial representations akin to a cognitive map. It is to note that despite presenting several chapters on bee learning and memory, the former book by Menzel and Mercer did not mention a single time the word ‘cognition’. It thus seems that the cognitive revolution has reached the bee as a model system, thus providing a novel glint to the already solid architecture of behavioral studies existing in this insect.

At a neural level, new approaches using imaging technology have emerged in these last two decades that allowed for simultaneous recording of neuronal assemblies, and that revealed spatial functional architectures in the brain. In this way both olfactory coding and more recently specific aspects of visual coding have been uncovered. In electrophysiology, although single-unit recordings are still fundamental to understand the properties of network components, new approaches based on multielectrodes have been developed that allow the simultaneous recording of many neurons at the same time with very high temporal resolution. Both approaches could be coupled with behavioral analysis *in toto* thus starting to reveal, in the case of olfactory learning, how and where olfactory memories are located in the bee brain.

Molecular biology has helped us to understand many new aspects of honeybee neuroscience. The honey bee genome has been sequenced so that genetic and molecular architectures underlying several aspects of bee behavior are now known. Yet, the advent of the genomic era with its panoply of sophisticated molecular techniques that are being adapted to the honey bee has yielded new challenges both for the molecular biologist, the neuroscientist and the behavioral biologist. For instance, olfactory and gustatory receptor genes have been identified in the honey bees but their specific ligands are still unknown. We also know that a bee has fewer genes involved in its immune system as compared to other insects, but which consequence should be derived from this fact is unclear.

All in all, a first level of response as to why this book would be necessary in 2011 is given by the fact that honey bee studies have made tremendous progresses in the last two decades and that it was therefore timely to cover this evolution in order to provide an integrative view on our current state of knowledge.

Finally, there is the personal tribute that this book wants to convey. The book is conceived as homage to Randolf Menzel and his long and productive career devoted to understanding multiple aspects of honey bee behavior and neurobiology.

Since Karl von Frisch, no researcher has covered with such a success so many aspects of the biology of the honey bee as Randolf Menzel did. From color vision and its cellular bases, to olfactory learning and the formation of olfactory memories and their cellular and molecular bases, from large-field navigation to floral ecology, the profusion of topics covered in Randolf Menzel's career is truly unique and impressively rich. What is unique in him is the combination between the laboratory neurobiologist and the field researcher, between the molecular biologist interested in the intracellular cascades underlying memory and the ecologist who travels around the world studying floral coloration in order to understand the neural bases of color vision. The original combination of behavioral, neurobiological, pharmacological, molecular, psychological and ecological approaches defines the richness of his multidisciplinary work. In his institute, he established long ago a rule that had to be respected: any student willing to work on neural or molecular levels in the laboratory had to perform at least once a field experiment on bee navigation in order to appreciate the complexity, plasticity and richness of honeybee behavior in a natural context. Copying from the richness of discussions in his group, we have designed a new format for this book: after each section, Randolf Menzel contributes with a dedicated commentary, putting the various aspects into a timeline joining past and not yet foreseen future, and making this book not only a collection of the state-of-the-art, but a real workbook for future research.

All three of us, former disciples of Randolf Menzel, wanted to celebrate through this book the life's work of our former mentor. We believed that such esteem was extensive to many other colleagues that did not work directly with him but who nevertheless appreciate the richness of his contributions. We were right in this conclusion as many coauthors joined us in this initiative to produce this book. We all coincided in acknowledging that Randolf Menzel is a passionate researcher, a researcher having devoted his life to understanding a mini brain which has uncovered some of his mysteries thanks to his work. Despite of this, we – including him – all know that there are still many, too many, questions to answer.

We really wish that this book will enlighten the pathways to take in order to find such answers. If there is a lesson to be taken from this book and from the research work contributed by Randolf Menzel is that Karl von Frisch was right when he called the honeybee a magic well – no matter how much is discovered, more remains to be uncovered.

Let us end with thanking all those who made this book possible: our friends and colleagues who joined us to celebrate the 70th birthday of Randolf Menzel in June 2010, the authors of the chapters, who took the care of writing these excellent texts, Ignacio (Nacho) Malter Terrada for the cover art (we are sorry that the publisher could not print it on the external cover for commercial reasons), and especially Mihaela Mihaylova for the impressive amount of work in the production of the book, assuring the highest standards of quality.

Martin Giurfa
Dorothea Eisenhardt
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Part I
Mechanisms of Social Organization

Chapter 1.1
The Spirit of the Hive and How a Superorganism Evolves

Robert E. Page, Jr.

Abstract Social insects presented Darwin (1859) with major difficulties for his fledgling theory of evolution by natural selection. How could differential survival and reproduction result in sterility, differential anatomy and behavior between sterile workers and queens, and differentiation among the sterile individuals of a colony? Maurice Maeterlink, Belgian author and Nobel Laureate, wrote (in 1901) about the "inverted city" of the honey bee noting that there is no central authority, that order and organization is achieved mysteriously through what he called the "spirit of the hive" [Maeterlink M, The life of the bee. Dodd, Mead, and Company, New York, 1913]. William Morton Wheeler [J Morphol 22:307–325, 1911; The social insects. Harcourt, Brace and company, New York, 1928], Harvard entomologist and philosopher, proposed that insect societies are true "superorganisms" because they are organized for nutrition, reproduction and defense, a view that was initially supported by biologists but lost favor by the early 1970s. Hölldobler and Wilson resurrected the superorganism in their book *The Superorganism: the Beauty, Elegance, and Strangeness of Insect Societies* [W. W. Norton, New York, 2008]. However, fundamental questions remain about the evolution of insect societies as superorganisms. Not only is there order without central control (the spirit of the hive), there is also no central genome on which natural selection can operate to sculpt a social system. Here, I will locate and define the honey bee "spirit of the hive" and show how selection operating on social traits involved in colony nutrition, a superorganismal trait of Wheeler, changes the genome, development, physiology, and behavior of individual workers that affect the "spirit of the hive" and, therefore, social organization.

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