Preface

Karen A. Mesce

Departments of Entomology and Neuroscience, and Graduate Program in Neuroscience, University of Minnesota,
St. Paul, Minn., USA

The ‘Modulation of Neuromodulators’ is the theme uniting the five contributions to this special issue of *Brain, Behavior and Evolution*, and served as the focus for a symposium held at the Sixth International Congress of Neuroethology, in Bonn, Germany, during August of 2001. The general topic of discussion was how potent chemical modulators of behavior are themselves ‘modulated’ by a variety of influences including: social and developmental events, hormones and other neuroactive substances, parasitism, and specific network configurations. By addressing how the physiology and external world of an animal can shape the suite of neuromodulators that regulates the activity of the nervous system, participants underscored the importance of such metamodulation for behavior. This emphasis on second-order modulation, observed across a number of different animal preparations, highlights the capacity of such regulatory mechanisms to expand the operational range in which animals can behave adaptively.

The chosen topic for the Symposium in Germany was one that had been simmering in my mind for quite some time, and one that had begun to appear as a common thread unifying the various studies conducted in my own laboratory. My initial appreciation of neuromodulation and its importance for behavior was enthusiastically guided by my doctoral thesis advisor, the late Graham Hoyle (University of Oregon, Eugene), who often discussed with me his ideas about the organizational roles of octopamine (the analog of norepinephrine) in inverte-

brate systems. Although I did not begin to study this neuromodulator until a decade later, Hoyle’s compelling ideas have clearly shaped my ideas about how octopamine and other biogenic amines can orchestrate behavior. In all the manuscripts [Mesce, 2002; Schulz et al., 2002; Edwards et al., 2002; Adamo, 2002] but one the significant neural and behavioral roles of octopamine and serotonin are revealed. The research presented by these authors on the second-order modulation of the biogenic amines should broaden our thinking about the diverse mechanisms underlying behavior and its flexibility. The final paper of the series, by Nusbaum [2002], addresses the mechanisms underlying behavioral flexibility at the level of identified neurons and neural circuits, and discusses how synaptic interactions and peptidase activity can serve to regulate peptidergic signaling and motor pattern generation.

Overall, the series of papers presented in this issue reflect the organizational flow of topics presented at the 2001 Neuroethology meeting in Bonn, although the contribution by Shelley A. Adamo [2002] was added after that meeting. Several sub-themes unite the first two papers by Karen A. Mesce (University of Minnesota) and David J. Schulz et al. (University of Illinois). In both the moth and honey bee systems described, respectively, the levels and expression patterns of octopamine appear to be regulated by developmental and lifestage-specific events contributing to the expression of particular adult-specific behaviors. For example, the steroid hormone 20-hydroxyecdysone (20-E) was demonstrated to influence octopam-

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Dr. Karen A. Mesce
Department of Entomology, University of Minnesota
219 Hodson Hall, 1980 Folwell Ave.
St. Paul, MN 55108 (USA)
Tel. +1 612 624 3734, Fax +1 612 625 5299, E-Mail mesce001@tc.umn.edu

ine expression during development of the moth *Manduca sexta*, and affect the developmental plasticity of octopamine synthesis and the production of new octopamine-immunoreactive neurons. These events have been postulated to contribute to the expression of behaviors specific to the adult stage. Schulz et al. [2002] discuss how octopamine levels in the honeybee become elevated during the normal developmental progression of bees shifting from hive workers to food foragers. Social factors that affect this shift also influence the levels of octopamine in the antennal lobes of worker bees, suggesting an interaction between social environment and the octopamine-mediated modulation of behavior. These results indicate that brain amine systems in the honey bee are sensitive to a range of both intrinsic and extrinsic influences.

A continued discussion of social interactions and their influence on the actions of the biogenic amines was led by Donald H. Edwards (Georgia State University, Atlanta). The paper by Edwards et al. [2002] describes how the abrupt decision of one of two fighting crayfish to escape can determine the social hierarchy of two crayfish, with the escaping animal identified as the new subordinate and its opponent as the new dominant. Maturation of this hierarchy is marked by a reduction in the frequency of aggressive interactions as the subordinate comes to avoid the dominant. These behavioral changes are thought to result from modulator-mediated changes that alter the relative excitability of neural circuits regulating discrete behaviors. Two socially-related changes were identified in crayfish: alterations in the pattern of serotonin release and the distribution of serotonin receptors that affects escape behavior. In addition, continued studies by Edwards et al. and Mesce and her colleagues, as reported in this issue, emphasize the novel and complex ways in which the actions of serotonin can be altered via second-order modulation.

Interestingly, the modulation of neuromodulators also provides a strategy capitalized by parasites to control the behavior of their invertebrate hosts. The report provided by Shelley A. Adamo (Dalhousie University, Halifax) reviews how various parasites can manipulate their hosts' biogenic amines and neuropeptides to alter host feeding and other motor activities. By altering the levels of neuromodulators manufactured by the host, sometimes by way of the host's immune-related response, at least some parasites have evolved an energetically cost effective adaptation to control the behavioral repertoires of their doomed hosts.

The final paper contributed by Michael P. Nusbaum (University of Pennsylvania) brings the focus of second-order neuromodulation to the level of identified circuits and synapses. Not much information has been available regarding the extent to which there is uni- or bi-directional communication between descending modulatory projection neurons and the neural circuits they control. By using the stomatogastric nervous system of the crab *Cancer borealis*, it was documented that neuronal circuits do indeed provide functionally important synaptic feedback that regulates the activity, and therefore the influence, of modulatory projection neurons. One function of this feedback is to enable one neural circuit (the pyloric circuit, which generates the rhythmic neural activity underlying the filtering of chewed food) to regulate and coordinate the activity of a distinct but behaviorally-related neural circuit (the gastric mill circuit, which generates the chewing motor pattern). Specifically, this feedback enables the pyloric circuit to control the speed of the gastric mill rhythm and its across-pattern coordination. Lastly, the pattern of firing activity of neurons containing multiple transmitters, including peptide modulators, together with the differential presence of peptidases within the synapse, help to sculpt the precise modulatory actions of projection neurons.

I will end by heartily thanking the organizers and program selection committee of the Sixth International Congress of Neuroethology for including our symposium in the Bonn meeting, and the contributors to this issue with whom it has been a great pleasure to work. My gratitude also goes to Walt Wilczynski for his enthusiastic support of this issue, to Blinda McClelland for her welcomed assistance in the preparation of this publication, and to my friends and colleagues who helped with the peer-review process.

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