

Editorial

The role of monoamines in modulating behavior

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Introduction

Understanding the mechanisms underlying complex behaviors requires a comprehensive investigation of the neurobiological factors that regulate and modulate their expression. Monoamines, such as serotonin, dopamine, and noradrenaline, serve a variety of essential physiological roles in modulating animal behavior. Furthermore, the evolutionary conservation of these aminergic systems spans across both vertebrates and invertebrates, having comparable effects in such diverse processes as learning and memory, aggression, mating behaviors and reproduction, stress responses, locomotion, and collective social behaviors (Dishman 1997; Libersat and Pflueger 2004; Kamhi and Traniello 2013; Bubak et al. 2014a; De Boer et al. 2015). Outstanding research is currently being conducted in this field, uncovering remarkable similarities in neural circuitries even among highly divergent taxa, such as *Drosophila* and humans. Investigating the neural mechanisms involved in the monoaminergic modulation of behavior across a variety of taxonomically distant species can provide researchers with a better understanding of the origins and functions of these systems. The goal of this special issue is to provide a venue in which colleagues studying similar questions across highly divergent animal systems can present their recent and groundbreaking work in this exciting area of biology. We hope this collection of papers will encourage and stimulate a dialogue on the similarities of monoaminergic function in a wide variety of animals and ultimately promote future comparative approaches when investigating behavioral modulation.

Current Research Integrating Monoamines and Behavior

In this issue, we aim to highlight a range of animal models systems to illustrate the central role that monoamines play in modulating various behaviors. This special column features seven contributions drawn from the participants in a symposium we organized for the 9th International Congress of Comparative Physiology and Biochemistry, held in Krakow, Poland, in August 2015. Featured animal models include both invertebrates and vertebrates.

Synthesis, new directions, and reviews

The issue starts with a synthetic contribution by Bubak et al. (2016), who use a well-established model system for aggression, stalk-eyed flies (Bubak et al. 2014a), to investigate the role of monoamines in assessing opponent resource-holding potential in aggressive interactions. Using large, published data sets (Egge and Swallow 2011; Egge et al. 2011; Bubak et al. 2014b), they aim to distinguish between two commonly used models of assessment strategies, self-determined persistence and mutual rival assessment, as described by Taylor and Elwood (2003). Bubak et al. (2016) clearly demonstrate that assessment strategies, decisions regarding whether to escalate aggression or retreat, and contest outcome are better predicted when behavioral and neurophysiological measurements are incorporated alongside morphological indices of resource-holding potential.

Eusocial insects, including ants, self-organize to solve complex problems, and biogenic amines play a significant role in the neuro-modulation of social behaviors (Kamhi and Traniello 2013). In the second conceptual piece of this issue, Hoover et al. (2016) develop an individual agent-based model that illustrates how individual changes in brain concentrations of the biogenic amines serotonin and octopamine, coupled with a simple inherent decision rule, can explain the escalation of individual aggressive acts to colony wide warfare. This model makes specific predictions about the proximate neurochemical mechanisms underlying the process leading to a collective decision and escalation to war. This approach has the potential to inform and direct specific mechanistic studies that examine how individual decisions can lead to complex, self-organized behaviors.

The issue ends with a comprehensive synthetic review of the role of serotonin in modulating fish behavior (Winberg and Thornqvist 2016). Specifically, the authors describe how the brain serotonergic system is involved in phenotypic plasticity and how different environmental factors shape the behavior of an individual under this context. In one example, the authors describe divergent stress coping styles (proactive vs. reactive) observed within teleost fish as well as other vertebrates. The stark contrast between the two behavioral phenotypes seems to be modulated in part by serotonergic mechanisms. The reactive fish, typically found to be shy and less aggressive, have elevated synthesis and metabolism of serotonin following

stress, whereas the more dominant and routine-prone proactive fish do not. Investigating the underlying monoaminergic mechanisms that mediate behavioral syndromes will provide great insight into this field.

Empirical studies of the role of monoamines in complex behaviors

Stevenson and Rillich (2016) provide a nice synopsis of their proliferative work investigating the roles of biogenic amines and nitric oxide in cricket aggression. In a series of convincing studies, Stevenson and colleagues specifically uncover the role of the insect analogue to noradrenaline, octopamine, on the adaptive decision to fight or flee. Using pharmacology, the authors discovered that octopamine could be considered the motivational component of aggression, demonstrating a necessary role for the biogenic amine in resource possession-inducing aggression. At the opposite behavioral response, Stevenson and colleagues convincingly demonstrated a suppressing, flee-promoting role for nitric oxide as well as its role in the loser effect.

In another evolutionarily important behavior, Panaitof et al. (2016) provide novel insight into the neuromodulation of biparental care for offspring in the burying beetle *Nicrophorus orbicollis*. This remarkable behavior is characterized by a synchronous shift in male and female behavior, coordinating effective care for their offspring by burying a small animal carcass as food for their larvae as well as other demanding parental activities. The authors investigated the role of several monoamines including serotonin, octopamine, and dopamine during this reproductive stage. They provide novel evidence for the role of dopamine in the modulation of burying beetle parental behavior, showing a sharp increase in levels following 24 h of care. Interestingly, whole brain levels of serotonin and octopamine were unaltered compared with nonbreeding pairs.

The health benefits of regular exercise, as well as the contrary deleterious effects of a sedentary lifestyle, are well documented. These effects are known to impact the nervous system and seem to be conserved across vertebrate species. In terms of neurophysiology, the monoamines serotonin and noradrenaline have been extensively studied for their anxiolytic and anti-depressive effects following exercise. Nicastro and Greenwood (2016) effectively and succinctly review this information while also discussing current limitations in research and future strategies. Additionally, the authors provide a novel hypothesis regarding the mechanisms of the emotional effects of exercise via the activation of a subset of temperature-sensitive serotonergic neurons in the dorsal raphe nucleus.

Jaromin et al. (2016) investigated the role of dopamine and noradrenaline on exercise performance. Specifically, the authors studied the underlying motivational mechanisms associated with increases in aerobic exercise performance. The authors artificially selected a population of bank voles to create selected lines of individuals with a high swim-induced aerobic metabolism, which achieved significantly higher metabolism than unselected lines. While successfully demonstrating baseline differences in aerobic exercise performance from the 2 selected lines, the authors did not see a conclusive difference in exercise performance following administration of the dopamine and noradrenaline reuptake inhibitor, bupropion. One possible explanation the authors raise for this lack of response could be the animal's ability to cope with stress. For example, the selection experiment could have acted on the individual's stress response rather than on motivation. Nonetheless, the authors provide important insight into inconsistencies seen among different animal models. This provides an example of the significance of investigating behavior and its

underlying neurophysiological mechanisms in a variety of animal species that may experience various evolutionary selection pressures.

Summary

The contributions to this special issue demonstrate the essential roles of monoamines in modulating animal behavior as well as the deep evolutionary conservation shared among taxa as diverse as humans and insects. Taken together, this collection of papers introduces the complexity of such studies and the importance of continued research. While much is known about the general role of specific monoamines and their subsequent behavioral outputs, the more proximate mechanisms, such as the underlying genetic basis and receptor subtype functions, remain less understood. We anticipate that the empirical studies as well as the synthesis articles in this collection of work will stimulate new ideas and approaches to investigate the essential underlying monoaminergic mechanisms mediating complex behaviors.

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