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Neurobiology of behavior

Editorial overview

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Russell D. Fernald is professor of Biology and the Benjamin Scott Crocker Professor of Human Biology at Stanford University. He joined the Stanford faculty in 1991 from the University of Oregon where he was a founding member and director of the Institute for Neuroscience. His research is focused on how social behavior is transduced into cellular and molecular changes in the brain using techniques from behavior to molecular biology.

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Constance Scharff is professor of Animal Behavior at the Freie Universität Berlin, Germany. She moved from the Rockefeller University to the Max-Planck-Institute for Molecular Genetics Berlin in 2001 before joining the FU faculty in 2004. Work in her laboratory has contributed to elucidate mechanisms and functions of learned vocal communication. Her current research investigates genetic and behavioral parallels between bird song and human language, focusing on the *FoxP2* gene.

This issue focuses on the neurobiology of social behavior. Animal species interact to reproduce, and sex requires at least some social communication. So the evolution of social behavior, including communication, evolved largely due to the selective pressures of reproduction. ‘Social behavior’ has many connotations so we define it operationally as ‘interactive behavior among animals’. Feeding together in a group, for example, does not fit this definition *per se*, unless some form of communication also occurs. Social behaviors are widespread in the animal kingdom, reflecting their usefulness. Indeed, since interactions among animals ultimately affect fitness, social behavior evolved in response to natural and sexual selective pressures. For example, how did acoustic communication arise in different taxa? In their contribution, *Kelley and Bass* review the evolution of vocal production and perception and how these are influenced by social context. A recent proposal for the evolutionary emergence of vocal patterning is described and a variety of sensory mechanisms needed for decoding social signals reviewed. Several novel technical approaches, including analysis of experimentally reduced vocal systems and transient inactivation of candidate brain regions has advanced our knowledge of brain assignments for vocal communication.

When animals communicate, senders and receivers often do not share the same intentions. For instance, the goals of social communication for the purpose of reproduction differ considerably between females and males. Since females typically invest more resources, their interest is to determine whether the courting male’s message is honest and indicates fitness, whereas males will invest at the lowest effective signaling cost. So it is not surprising that female and male brains can differ considerably in the neural substrates involved in social behavior. Illustrating these points, *Wilczynski and Ryan* review the recent progress that has been achieved in frog and toad social signaling. Male anurans advertise their wares acoustically so females will seek them out and mate with them. The nervous system is biased toward conspecific signals and, more specifically toward particular features of conspecific signals. This biasing of responses is evident in the peripheral nervous system but is also apparent from the brainstem through to the midbrain. The frog auditory midbrain appears important for the control of behavioral responses to social signals and this may also hold true for other vertebrate groups. Males, being often more visibly or audibly active during courtship, have received considerably more scientific attention than females. Turning on eye toward the females, *Ferveur* shows in his review that female fruit flies play an important role in social interactions. Previous work focused on the obvious male courtship behaviors, that are easy to count and on female rejection behaviors, perhaps more difficult for male scientists to understand. Using fine-grained behavioral analysis, Ferveur identifies an important step in courtship in which the female may release a droplet that rapidly arouses the male. This work

reminds us of the importance of understanding the roles of all the players in any social interaction.

Which neural substrates serve sex-specific behaviors? *Stowers and Logan* summarize the importance of olfaction in regulating rodent social behaviors and review recent findings about the circuits responsible for male–female differences. Though males and females respond identically to food odors, they have distinct neural pathways dedicated to gender-specific chemicals. The special organ for detecting information important for sex is the vomeronasal organ that is the privileged signaling pathway for mammalian reproduction. Addressing the mechanisms how female and male neural systems eventually turn out to be different, *Forger and de Vries* focus on cell death as a common effector across species that shape sex differences in the nervous system. As they discuss, we know most about the differences in cell number in specific nuclei associated with reproduction. However, less is known about the circuitry differences resulting from neural pruning during development. Using the naked mole rat, insights about how profound social signals can produce behavioral differences by changing the nervous system seem possible. Future work will focus on using the comparative method to understand the differences in circuits responsible for the behaviors.

Moving from circuits to molecules, *Goodson and Thompson* review the evolutionary origins of vertebrate nonapeptides and their phylogenetically ubiquitous effects on social behavior. The highly conserved neural pathways influence individuals and some of the pathways suggest feedback from peripheral body states to the brain. The functional integration of central and peripheral effects has made understanding the suite of complex interactions more difficult. Indeed, analyses of nonapeptide action in humans hint at their significant role in social interactions. Despite the diversity of actions, the authors' argue that there are sufficient commonalities across species to suggest emergence of a common understanding of the functional role they play. Staying with the theme of nonapeptide actions, *Phelps* centers his review on the relationship of the vasopressin 1a (V1aR) receptor to pair bonding. He argues that understanding subtle differences in phenotypes ('endophenotypes') can guide our understanding of complex behaviors in animals and humans and the variation in phenotype has made it difficult to dissect complex traits. However, recent work on the V1aR has linked it to both social attachment and patterns of sexual fidelity. Lab experiments showed that high V1aR expres-

sion in a particular brain area was necessary for male pair bonding. However, this is not true for animals in the field, where more complex interactions amongst V1aR and other brain neuropeptide systems are at play. The idea that expression levels of one receptor type leads to one behavioral phenotype may have resulted from the reduced social complexity of the testing methods rather than from a fundamental relationship. Clearly the V1aR receptor is important, but it is not the whole story. Commonalities between humans and non-human animals also exist in social status, the subject of the review by *Chiao*. She draws on data from many species, making the case that social status hierarchy is a ubiquitous principle of social organization from ants to fish to primates. In humans, she reports evidence that social status is represented in specialized areas of the brain different from those associated with social cognition. There is a suggestion that allelic variation in the serotonin transporter gene is associated with social hierarchies. Since perceived social rank has important influences on psychological and physical health, understanding how social status is represented could be important for understanding that link.

Concluding this issue is a review by *Bray and colleagues* who discuss the neurobiological underpinnings of schizophrenia, a severe psychiatric illness with diverse symptoms and an elusive definitive pathology. Although heritability estimates for schizophrenia are ~80%, genome-wide association studies have revealed no common genetic variants conferring an even two-fold increase in risk. However, some genes that predict liability for schizophrenia have been identified and interestingly, some of these predict both schizophrenia and bipolar disorder susceptibility. It appears that thousands of common alleles with very small effects might, in aggregate predict some (30%) variation in schizophrenia risk.

Our goal in these reviews was to highlight the diversity of model systems and approaches used to study the wide variety of different social behaviors and their neural underpinnings. There are clearly common themes and mechanisms emerging, spanning surprisingly large phylogenetic distances, but important variations exist. In the end, it is possible that social interactions and communication involve a core set of neural processes and ultimately gene networks, be it via deep homology or convergent evolution. The future of research into the social brain looks interesting indeed.