Keeping Birds of a Feather Together

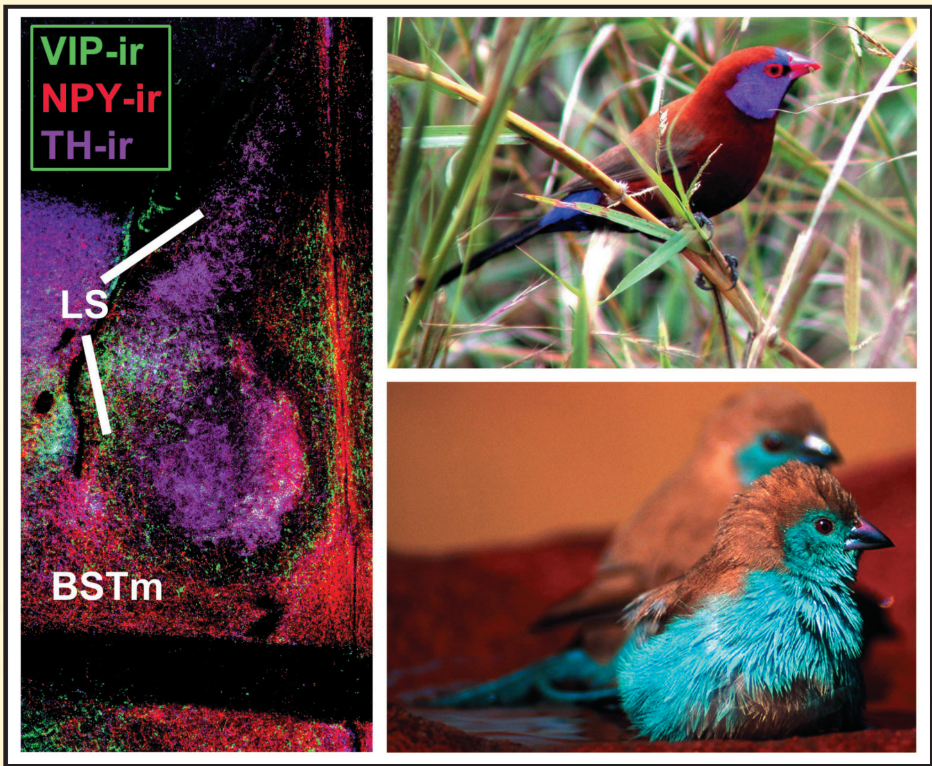
SUMMARY

Vertebrate species display extreme variation in grouping behaviors, ranging from solitary living to the aggregation of thousands of animals. Comparisons of territorial and gregarious species reveal differences in the distributions of several neuropeptide receptor types, primarily within the lateral septum, and the presence of neuropeptide neurons that encode social valence (positive-negative). Experiments show that these neural elements potently influence decisions about group size.

A science of party animals

From a solitary wolverine to a massive flock of migratory blackbirds, grouping behavior (or lack thereof) is central to how we perceive and classify species. It is also one of the most important aspects of behavior in terms of Darwinian fitness. However, until recently, the neurobiological mechanisms that influence an individual's preference for groups of a given size (or for no group at all) have not been a topic of investigation. This is likely because grouping is difficult to isolate from other aspects of ecology and behavior, such as mating system and patterns of parental care. For instance, rodent species that differ in their grouping behaviors also tend to differ in whether they are monogamous or polygamous, and whether the father contributes to parental care. This matters because shared neural mechanisms, particularly *neuroendocrine* mechanisms, often influence multiple aspects of social behavior (such as pair bonding, parental care and same-sex affiliation) and related aspects of physiology. Thus, if we want to see how brains function and evolve in relation to grouping, we need to control for as many other variables as possible.

Importantly, although "sociality" and "affiliation" are increasingly popular topics of study, these terms are often used in a very broad way, which may lead us to believe that all aspects of sociality are regulated as a unitary output and evolve in a linked fashion. However, if we look



The complex chemical anatomy of the lateral septum (LS; left panel) has remained stable for hundreds of millions of years, and is virtually identical in birds and mammals. However, the distributions and densities of nonapeptide receptors in the LS, which potently influence grouping, differ dramatically even within closely related species, such as the territorial violet-eared waxbill (top) and the gregarious Angolan blue waxbill (bottom).

at the diversity of social structures to be found in mammals and other vertebrates, it is clear that behavioral variables such as species-typical group size, mating system, patterns of parental care, and affiliation behaviors (such as the extent of physical contact and grooming) evolve in an almost cafeteria-style fashion. Furthermore, as described below, neural mechanisms that promote preferences for larger groups ("gregariousness") are not necessarily the neural mechanisms that promote social contact in the first place.

A bird-brained approach to grouping

As amazing as it may seem, social behavior circuits in the brains of birds and mammals are exceptionally similar, as established through a wide range of functional, molecular and anatomical studies. The lateral septum (LS) is a good example. In rats, this area can be subdivided into 20 zones that differ in their neurochemistry and position, and virtually all of these or their conglomerates can be recognized in songbirds (Fig. 1). Extensive similarities are also known for the medial extended amygdala, multiple nuclei of the preoptic area and hypothalamus, and associated structures that mediate incentive, reward and responses to stress.

Birds offer excellent opportunities to study grouping, because we can identify closely related species that are nearly identical in most aspects of behavior and ecology, but exhibit extreme variation in grouping. The finch family Estrildidae is a standout in this regard. All estrildids typically form life-long pair bonds and exhibit biparental care, but whereas most of the 141 estrildid species form small parties when they are not breeding and loosely distribute for nesting, a few species have evolved territoriality and several others are found year-round in large flocks of 100 or more birds.
Using five finch species (two territorial, one modestly gregarious and two highly gregarious), it has been shown that receptor distributions for corticotropin releasing hormone, vasoactive intestinal polypeptide, and the nonapeptides vasotocin and mesotocin (avian equivalents of vasopressin and oxytocin), all evolve in relation to species-typical group size, particularly within the LS.

> *"...social behaviour circuits in the brains of birds and mammals are exceptionally similar..."*

Thus, species that independently evolved territoriality have converged on similar receptor distribution patterns, as have species that independently evolved extreme gregariousness. Notably, vasotocin cells in the medial bed nucleus of the stria terminalis (BSTm, a major source of vasotocin projections to the LS) exhibit an exquisite sensitivity to the valence of social stimuli, such that they increase their transcriptional activity in response to positive, affiliation-related stimuli, but not to negative or nonsocial stimuli. In fact, following exposure to a same-sex conspecific, territorial finches actually decrease the activity of the BSTm vasotocin neurons, whereas highly gregarious birds show a robust increase. Territorial birds do increase the activity of these cells if the stimulus is their mate, whereas gregarious birds fail to increase neuronal activity if they are bullied. Antisense knockdown of vasotocin production in the BSTm of zebra finches profoundly reduces preferences for large groups, and similarly, blockade of V_{1a}- and oxytocin-like nonapeptide receptors in the LS reduces large group preferences with no effects on the time spent in social contact.

A major remaining question is whether our results are predictive for other taxa. All of the neurochemical systems just mentioned influence myriad behavioral and physiological functions, thus we might expect that those systems may not evolve in exactly the same way with relation to grouping if other species-specific behavioral and physiological functions constrain the evolutionary process. This may occur if a given neural mechanism is under strong selection in relation to something other than grouping, such as mating system. At the same time, the neurochemical systems under study influence basic social behaviors across a wide range of vertebrates, suggesting that they may be common (even ubiquitous) targets of selection during social evolution.

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