Reproduction is unique among life processes: although it may not be required for individual survival, from the standpoint of evolution, it is the only life process that counts. In view of the strong selective pressures that have shaped reproductive behavior and which, we infer, account for the dazzling variety of reproductive strategies and mechanisms, it is logical for a comparative neurobiologist to ask: How has evolution shaped the neural substrates that underlie reproductive behavioral expression?

A large and enthusiastic gathering convened at the fourth annual Karger Workshop at the J.B. Johnston Club to consider the interaction of neural and endocrine mechanisms in reproductive development and expression. Our keynote speaker, David Crews, opened the symposium with a talk on the regulation of a process that is fundamental to sexual reproduction, the differentiation of organisms into males and females. The role of gonadal steroids in this process is well-known. Much less well known is the role of sensory cues, arising from either the physical or the social environment, that can determine gender in the absence of genetic sex information. These, and other examples of atypical reproductive mechanisms have led Crews to question the well accepted view of sex determination, which emphasizes hormonally induced organization of the male phenotype, with the female phenotype defined as the neutral, or 'default' condition. Instead, Crews offered a novel concept, that the male pattern is derived and imposed upon the ancestral female pattern.

Another process that appears to be fundamental to vertebrate reproduction is the regulation of sexual maturation and behavior by gonadotropin-releasing hormone (GnRH) neurons, which exhibit both hormonal and neural properties. L. Muske discussed the organization and evolution of GnRH systems in vertebrates. She speculated that GnRH systems arose three times in vertebrate evolution, and that the ancestral GnRH system of gnathostomes is not the well known septo-preoptic pathway but, rather, a newly discov-
ered population of cells in the midbrain region. The fact that placental mammals are the only vertebrate group in which the midbrain cells are not widely distributed points out the importance of examining diverse animals in order to define basic neural principles.

In mature animals, GnRH secretion induces the production of gonadal steroids, which in turn act on the brain. While much progress has been made in identifying where in the brain steroids act, much less is known about how the fundamental electrical properties of neurons are altered by steroids, probably because there are few systems that permit these investigations. Harold Zakon's presentation illustrated the contribution that comparative neurobiologists can make in developing alternative animal models. He uses weakly electric fish, in which electric organ discharges are characteristic of gender and reproductive state, and are controlled by steroid hormones, to study the long-term actions of sex steroids on membrane biophysical properties.

Gonadal steroid hormones are also secreted early in development, and have profound effects on sex differences in brain and behavior of adults. Arthur Arnold discussed similarities and differences between steroid mediated sexual differentiation in rodents and in the zebra finch. His research demonstrates the important principle that mechanisms present in one species may not be generalizable to others. The unexpected finding that the brain, not the gonad, is the primary source of estrogen in the zebra finch further illustrates the importance of comparative studies to gaining an appreciation of the full range of sexual reproductive mechanisms that have evolved.

That hormones are essential for reproductive behavior is well known. Somewhat less well appreciated is the influence that behavior - in the form of conspecific social signals - may have on hormone secretion and gonadal state. W. Wilczynski described the pathways by which social and other environmental information, such as day length, can
modulate the output of GnRH neurons in frogs. The strong dependence of these species on auditory signals from conspecifics during mating, and their comparatively simple brains, illustrate how multimodal sensory information needed to synchronize reproductive activity with appropriate physical and social factors may be centrally integrated. The role of intraspecific social signals in modulating both reproductive behavior and physiology, and the intricate functional links between neural and endocrine systems, was explored further in our final presentation. J. Dulka discussed a complex information cascade in goldfish, in which pheromones, an endocrine product, serve as sensory signals which act on the nervous system of con-
specifics and influence both reproductive behaviors and hormonal state. Dulka also compared the neural pathways that mediate olfactory, including pheromonal, cues in teleosts and tetrapods and raised the question of whether teleosts possess a functional correlate of the vomeronasal system in tetrapods.

If the main achievements of evolution are in the realm of behavioral: complexity, then the main behavioral achievements are probably those related to reproduction. The enormous diversity in vertebrate reproductive patterns offers a rich source of natural experiments that can yield new insights into brain structure, function and evolution, besides providing numerous topics for future workshops.