

From Fertilization to Adult Sexual Behavior¹

Milton Diamond,* Teresa Binstock,† and James V. Kohl‡

*Department of Anatomy & Reproductive Biology, John A. Burns School of Medicine, University of Hawaii–Manoa, Pacific Center for Sex and Society, 1951 East–West Road, Honolulu, Hawaii 96822; †Developmental & Behavioral Neuroanatomy, Fragile X Section, B140 The Children's Hospital, 1056 East 19th Avenue, Denver, Colorado 80218; and ‡Simtex, 2950 East Flamingo Road, Suite J, Las Vegas, Nevada 89121

Research has established the broad mammalian developmental plan that genes on the sex chromosomes influence gonad development which determines gonadal hormone production (or its absence) leading to modification of the genitalia and simultaneously biasing the nervous system to organize adult sexual behavior. This might be considered the "gonad to hormones to behavior" model. It is clear, however, that although this model generally works well it is incomplete. The model does not account for behavioral influences attributed to the environment or to genetic but nongonadal or hormonal factors. In this essay we probe those areas of sexual development that are neither differentiated by hormones nor activated by them. The concept of the environment used for our discussion is very broad; it incorporates considerations of both the molar and the molecular levels. The general sense of the word "environment" as something exterior to the person is retained, even if that something influences intraperson processes. In addition, we focus directly on molecular events themselves. Here the "environment" involved can be that within a DNA segment. We also expand the notion of "biologically based sex differences." Although many, and perhaps most, important sex differences arise from gonadal and hormonal development, also important are sex differences which are neither gonadal nor hormonal. All these factors affect the internal workings of the individual and intervene in structuring how the social environment might or might not modify sexual behavior. This discourse calls attention to features that are central to the so-called nature–nurture discussion. © 1996

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¹ This paper is dedicated to Robert (Bob) W. Goy, upon his retirement. Bob himself dedicated much of his life to understanding sexual behavior.

. . . nature versus nurture, the old battlefield destined to be revisited by every generation of scientists struggling to uncover the mysteries underlying behavioral mechanisms.

Ingeborg L. Ward (1992)

. . . the nature/nurture debate is much more than simply a scientific argument. It is a clash of cultures, of ideologies and of politics.

Robert Pool (1994)

As the millennium approaches and a respected leader in our discipline retires at about the same time, it is fitting to reflect on some seminal issues in the field of behavior. One major issue is to comprehend, particularly in regard to behavior, factors which are important influences on sexual expression and the development of sex differences. A series of major breakthroughs occurred some four decades ago that had many, at least among the more biologically minded behaviorists, believing that such an understanding would soon be with us. Unfortunately, the feeling was premature. It is the purpose of this discourse to discuss aspects of sexual development and to offer insight as to why understanding such processes is much more complicated than initially assumed.

Historically one of the first breakthroughs was the determination by Jost and colleagues (Jost, 1953, 1961) that the fetal gonad, responding to its genetic endowment, elaborates substances that can influence the development of the internal and external genitalia. A second milestone can be considered the findings, in 1956 by Tjio and Levan, that the typical human chromosomal complement contained 46 chromosomes: 44 autosomes and the sex chromosomes, XX for females and XY for males. This clarification of basic genetics gave hope that further related discov-

eries would soon follow. A third milestone was provided by the findings of Phoenix, Goy, Gerall, and Young (1959) that endogenous prenatal hormones are crucial in the organization of adult sexual behaviors. Such hormonal actions were seen powerful enough to structure (*organize*) behavior patterns that would be manifest (*activated*) at puberty or after.

These now-classic papers, along with many others, established the broad developmental plan that, at least for mammals, the following pathway occurs: genes on the sex chromosomes influence gonad development which determines gonadal hormone production (or its absence) leading to modification of the internal and external genitalia and simultaneously biasing the nervous system to organize adult sexual behavior (see e.g., Goy and McEwen, 1980). Even body morphology was supposed to follow along with this paradigm of sexual differentiation. This might hereafter be considered the classical "gonad to hormones to behavior" (Gd-H-B) model.

It soon became clear, however, that although this model worked well in broad strokes it was incomplete; many exceptions were obvious. For instance, the model did not account, in as ready a way, for other possible influences; i.e., those attributed to the environment or to genetic but non-Gd-H-B factors. For example, even among monozygotic twins reared together, while indeed most do parallel each other for as basic a trait as sexual orientation, a significant number are not concordant for androphilia or gynecophilia or even body configuration (Bailey and Pillard, 1995; Whitam, Diamond, and Martin, 1993). Clearly, additional factors intercede in the path from fertilization to adult phenotype.

Some further questions seemed to also arise to challenge a simple Gd-H-B paradigm. For instance, if prenatal androgens modify morphology directly and sexual behavior indirectly via the nervous system, why do we see some very masculine appearing men who are androphilic and some feminine appearing females who are gynecophilic? Either (i) homosexual effeminate males and masculine females or (ii) heterosexual masculine men and effeminate women would seem to better fit the model. Similarly the model does not account for individual women with the complete androgen insensitivity syndrome (CAIS) who are gynecophilic.

Typically, experiments to probe the workings of the Gn-H-B model introduce hormones or other drugs to prenatal or parnatal animals and then test them later in development. We will not go into that large body of data here. One set of studies, however, deserves mention since, like the human findings mentioned above,

it directly challenges Gn-H-B expectations. Goy, Bercovitch, and McBrair (1988) exposed female fetuses to testosterone propionate either early or late in gestation. Their results indicate that the genitals of the early androgen treated females were virilized and those of the late treated females were not. Behaviorally, the late treated females, unlike the early treated ones, showed male-like elevated rough play and mounting with peers and the absence of a preference for male partners. The early treated females did not show such behaviors. These results indicate the androgen given to the late treated females altered their sexual preference as well as play and mounting behaviors without altering their genitalia. The early treated females, in contrast, had their genitals altered but not their sexual preferences. The structure of the genitals did not coincide with the sexual behavior displayed. Other experiments revealing discrepancies in the simple Gn-H-B model can be cited. These results have implications relative to different human conditions such as transsexualism, the congenital adrenogenital hyperplasia (CAH) syndrome, intersexualism, and perhaps homosexuality as well.

Interestingly, while mammals do seem to at least generally follow the Gn-H-B model, other vertebrate genera such as fish and amphibia follow a different one. In many of these species the paradigm which evolved is more like: genes prepare the individual to react to the environment which will bias the nervous system which will then lead to gonadal development and hormone release and this will influence adult behavior. A further significant difference between these two models is that, for mammals, once adulthood is reached, the processes are relatively fixed. Among many nonmammalian species, on the other hand, this is not so. The individuals can remain quite sensitive to the environment. Two examples are illustrative. Among certain turtles, females will develop at extreme hot and cold temperatures and males at moderate temperatures (Bull, 1983; Gutzke and Paukstis, 1984; Yntema, 1976). The reef fish *Thalassoma duperrey* is usually born as a female with appropriate coloration, behavior, and production of eggs. If there is no larger male in her visual vicinity, and there is a smaller conspecific female nearby, she will become a sperm producing male with male coloration and behaviors (Ross, Losey, and Diamond, 1983). We predict that humans will basically follow the mammalian model but maintain aspects of evolutionary development which show sensitivity to environmental influences.

Goy and McEwen (1980), for mammals, have classified sex differentiated aspects of behavior into three

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