Sex hormones and sexual orientation in animals

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This review critically examines whether sex hormone exposure during prenatal or early postnatal development determines the adult sexual orientation (sexual preferences) of animals. In rats, hamsters, ferrets, pigs, zebra finches, and possibly dogs, either early castration of males or early testosterone treatment of females or both have been shown to change or reverse sexual orientation. The effects of early sex hormone exposure on copulatory behavior, studies of prenatal hormones and sexual orientation in humans, different animal models for research on sexual orientation, and the desirability of a broad psychobiological investigation of sexual orientation in animals are discussed.

The influence of sex hormone exposure during prenatal or early postnatal development on the sexual orientation of animals would seem to be an obvious topic for research, yet this subject has received surprisingly little attention. Since the publication of Young, Goy, and Phoenix's (1964) influential paper outlining an organizational theory of behavioral sexual differentiation, a great deal has been learned about how sex hormones produced during the neonatal period determine sex differences in copulatory behavior, but much less attention has been given to the possibility that these early hormones might influence not only how frequently animals copulate or what motor pattern they exhibit in a sexual interaction, but also which sex they choose to spend sexual time with. In the past few years, however, there has begun to be a significant body of work on early sex hormones and sexual orientation in animals.

A review of this literature is timely because of increasing interest in the possibility that human variation in sexual orientation has a prenatal sex hormone basis. The most complete and explicit statement of the theory that prenatal hormone exposure determines who will be heterosexual, homosexual, or transsexual has been made by Dörner (1976; see also Dörner, 1988, for a more recent summary). Several studies of humans have been interpreted as lending support to this theory (see reviews by Ellis & Ames, 1987; Meyer-Bahlburg, 1984; Money, 1987; and the report by Gladue, Green, & Hallman, 1984). There are many problems with these experiments that have already been succinctly summarized (Baum, Carroll, Erskine, & Tobet, 1985; Gooren, 1984; Meyer-Bahlburg, 1984), and there have been difficulties with replication (Gooren, 1986; Gooren, Rao, van Kessel, & Harmsen-Louman, 1984). In addition, the human literature assumes that early sex hormones have been shown to determine

sexual orientation in nonhuman animals. Is this the case? Most positive claims cite inappropriate experiments, indicating a need for a more critical review of the relevant animal literature.

TERMINOLOGICAL AND CONCEPTUAL ISSUES

Nonhuman animals (hereafter called simply animals), like most humans, show consistent courtship and mating preferences for either males or females. I will use the terms *sexual preferences* and *sexual orientation* nearly interchangeably to refer to this phenomenon, although in the ethology literature the term *sexual preference* is generally associated with experiments on animals' mating preferences for one species or color form versus another (e.g., Bateson, 1978). What is critical in determining an animal's sexual orientation/preference is that the subject be observed with stimulus animals of both sexes, preferably in some kind of choice situation. It is well known that if animals are tested only with same-sex partners, they will copulate with them, particularly if the subjects are sexually deprived or treated with heterologous sex hormones (ovarian hormones for males, testicular hormones for females) (Adkins-Regan, 1981; Feder, 1981; Young, 1961). But such observations do not necessarily mean that, given a choice, they would *prefer* to interact sexually with same-sex partners. Similarly, experiments measuring time spent by males with estrous versus nonestrous females or time spent with estrous females by intact versus castrated males, although interesting for understanding sexual motivation, are not relevant to the question as to whether early sex hormones determine sexual orientation.

Also, sexual orientation does not refer to the copulatory motor patterns that the animal performs. A male rat mounting another male is engaging in a homosexual interaction, but a female rat mounting a male is not. She is showing male-typical (heterotypical) behavior, but is interacting sexually with an opposite-sex, not same-sex, partner; she is engaging in a heterosexual, not homosexual, interaction.

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The serious conceptual error committed by confusing sexual orientation with the capacity for heterotypical behavior when exposed only to same-sex partners has been explained quite articulately several times (e.g., Beach, 1979; Davidson, 1979), yet the error persists. Of five recent reviews of the prenatal hormone hypothesis of human sexual orientation (Dörner, 1988; Ellis & Ames, 1987; Gooren, 1984; Meyer-Bahlburg, 1984; Money, 1987), only two were sensitive to these important distinctions (Gooren, 1984; Meyer-Bahlburg, 1984). Ellis and Ames (1987) cited nearly 40 published experiments on early hormone influences in animals that are supposedly relevant to a "neurohormonal" theory of human homosexuality. Only one of these (Ford, 1983a) actually measured sexual orientation.

It is also important to distinguish between sexual preferences and nonsexual social preferences. Adult female wild pigs, for example, travel together and interact with males only during the breeding season (Frädrich, 1974; Gründlach, 1968). In choice tests, such females might well prefer to spend time with females, but such results would have no bearing on mating preferences. Similarly, experiments in which the stimuli are odors taken from males versus females, rather than actual animals themselves, are not direct examinations of sexual orientation. The ideal sexual preference experiment would be designed to ensure that the primary motivation for the choice is sexual, and would reflect some knowledge of the social organization of the species, as well as some understanding of the roles of the sexes in mate choice. In the species under study, does the female normally do most of the choosing? The male? Both?

Thus, this review focuses on experiments that actually determined sexually motivated preferences in choice situations involving male and female stimuli. Because the experiments that are discussed grew out of research on sexual differentiation of copulatory behavior, a brief and somewhat oversimplified summary of this process is appropriate (see Baum, 1979; Feder, 1981; Goy & McEwen, 1980). In mammals, testicular hormones, either androgens or estrogens derived from androgens, that are produced during prenatal or early postnatal development lead to male differentiation by masculinizing behavior (increasing the capacity for male-typical behavior such as mounting) or defeminizing behavior (decreasing the capacity for female-typical behavior such as lordosis) or both. The relative importance of masculinization versus defeminization in male development depends on the species and on which type of copulatory behavior is more dimorphic, male-typical, or female-typical (Baum, 1979). In the absence of testicular hormones, female differentiation occurs; thus the ovaries do not seem to be critical for female behavioral development. Experimentally, females treated early in development with testosterone (T) or even estradiol (E) grow up to be male-like; compared with neonatally untreated controls, the adult females show high levels of mounting following priming with T and/or low levels of receptivity following priming with E or E

plus progesterone (P). Males castrated early in development grow up to be female-like; as adults they show low levels of mounting following priming with T compared with controls and/or high levels of receptivity following priming with E or E plus P. These sex-reversing effects of early gonadal hormone manipulations are permanent and are usually possible only during a critical period in neonatal development. For this reason, they are often referred to as "organizational" effects, as opposed to the temporary "activational" effects of sex hormones administered in adulthood.

Studies of organizational effects of sex hormones on copulatory behavior have established that male-typical and female-typical are separate behavioral dimensions, and that masculinization (increase in male-typical behavior) can occur independently of defeminization (decrease in female-typical behavior), and vice versa (Feder, 1981). In theory, and if the right experimental measure is used, male-typical and female-typical sexual preferences can also vary independently. In most studies, however, they cannot, because tests are fixed in length, and time spent with one sex is time that cannot be spent with the other sex. If testosterone-treated females spend more time with females and less time with males than do controls, should the effect be called masculinization or defeminization? I will use the term *masculinization* for any effect that causes females to become more male-like, and *feminization* for effects that cause males to become more female-like.

RATS (*Rattus norvegicus*)

Experiments on rats are often cited in support of hormonal theories of human sexual orientation. Wild Norway rats live and reproduce in groups (Robataille & Bouvet, 1976). Behavioral and physical dimorphism is slight, rather than pronounced. The mating system of wild rats is unknown, but, like most mammals, they are unlikely to be monogamous or to form pair bonds (Kleiman, 1977). When domestic rats are observed mating in groups, females mate with more than one male, and males mate with more than one female (McClintock, 1987). Both sexes actively court, and if there is any mate choice, probably both sexes choose mating partners.

There have been two extensive investigations of the sexual preferences of normal intact adult rats (Hetta & Meyerson, 1978; Meyerson & Lindström, 1973), as well as several studies of the effects of different adult hormone treatments on sexual orientation (i.e., activational effects; see below for specific references). A variety of methods and types of apparatus have been used, including double-choice runways or T-mazes, shock grids between the subject and the stimulus animal, arenas with stimulus animals in wire-mesh cages either inside or positioned around the outside, and arenas with tethered stimulus animals. In some of the experiments, the subjects were not actually allowed to have full physical contact with or to mate with the stimuli, so that the measures would more accurately reflect appetitive/motivational aspects of mating prefer-

ence unconfounded by consummatory aspects. Stimulus animals were sexually active intact males or ovariectomized females brought into heat with E plus P.

Intact females prefer males over females, and intact males prefer estrous females over males (Hetta & Meyerson, 1978; Meyerson & Lindström, 1973). Female sexual preferences are determined in part by the hormonal status of the rat at the time of testing; the preference of females for stimulus males is reduced by ovariectomy and increased by injection with E (de Jonge, Eerland, & van de Poll, 1986; Meyerson & Lindström, 1973; Slob, de Klerk, & Brand, 1987).

Three experiments compared the effects of different adult sex steroid treatments on the sexual orientation of adult ovariectomized females. Slob et al. (1987) found that females injected with 0.4 mg testosterone propionate (TP) three times per week showed weaker preferences for males than females given 20 μ g estradiol benzoate (EB) three times per week (a 20:1 ratio of TP:EB). However, de Jonge, Eerland, and van de Poll (1986) and de Jonge, Kalverdijk, and van de Poll (1986), using doses of TP and EB matched for activation of lordosis (1 μ g EB and 500 μ g TP, a 500:1 ratio of TP:EB) and giving only a single injection, found that TP was *more* effective for increasing the preference for males; that the synthetic androgen R1881, which cannot be converted to estrogen, readily stimulated the preference for males as well, but failed to activate lordosis; and that P given to EB- or TP-primed females facilitated both receptivity and proceptivity (hopping and darting) but not preference for males. These results suggest that the mechanisms for sexual preference and for receptivity/proceptivity are different. Such a dissociation is also indicated by an experiment (Dudley & Moss, 1985) in which ovariectomized females received estrogen priming plus third ventricle infusion of luteinizing hormone releasing hormone (LHRH). LHRH enhanced receptivity but did not increase preference for males in a choice apparatus, in spite of the fact that P following estrogen priming did increase preference for males in the same apparatus. The greater effectiveness of P in the Dudley and Moss (1985) experiment than in the de Jonge, Eerland, and van de Poll (1986) experiment is probably due to the 25-fold greater dosage used.

The adult hormone environment interacts in important ways with sexual experience to determine the sexual orientation of female rats. In the Slob et al. (1987) experiment, TP-treated females did show a preference for males, but after being allowed to interact with a freely moving male, they switched to a preference for females. De Jonge, Burger, van Haaren, Overdijk, and van de Poll (1987) compared the sexual preferences of experienced versus naive females ovariectomized as adults and given oil or TP. Naive females receiving oil showed no preferences; when treated with TP, they preferred males. But females with mount experience (experience with females) preferred females, regardless of whether they received TP as adults. In contrast, oil- or TP-treated females given sexual experience with males showed no preferences. It will be important for researchers to look at the interac-

tion between sexual experience and mate choice in females receiving homologous hormones (E plus P) as adults.

Less is known about the hormonal basis of male rat sexual orientation. The preference of males for estrous females over males occurs even without prior sexual experience, and is reduced by castration and increased by injection with T (Hetta & Meyerson, 1978).

Thus, there is good background information about the sexual preferences of rats, the role of adult activational hormones in the expression of these preferences, and the interaction between experience and hormones. These preferences are mediated in part by odors and the olfactory system (Carr, Loeb, & Dissinger, 1965; Hetta & Meyerson, 1978). Remarkably little is known, however, about the sexual differentiation of these preferences. Only three studies have looked at the effect of neonatal hormone manipulations on adult sexual orientation. All three used a circular arena with a box containing a sexually active male versus a box containing an ovariectomized female injected with E plus P.

Eliasson and Meyerson (1981) studied intact males and males castrated within 24 h of birth; subjects were tested from 30 to 120 days of age. At 30 days, the intact males already slightly preferred the female. This preference increased with age; time spent with the female increased, and time spent with the male decreased. The neonatally castrated males tested at 70 days also preferred the female, but significantly less so. This experiment by itself is not sufficient to conclude that neonatal testicular hormones influence sexual orientation in rats, because the two groups were different hormonally at the time of testing as well as neonatally (neonatally castrated males did not receive hormone replacement); that is, activational and organizational hormone actions were confounded.

Meyerson, Eliasson, and Hetta (1980) examined the role of neonatal sex hormones in both sexes. In one experiment, females were given TP at 5 days of age or were untreated. Testing began at 200 days, 3–4 weeks after ovariectomy, and females were tested without hormone replacement, with EB, or with TP. Without hormone replacement, the females showed no preferences. With either EB or TP in adulthood, the neonatally androgenized females preferred stimulus females instead of males (Figure 1). In another experiment, males were castrated 24–36 h after birth, and some were given TP on Days 2 and 4 while others were not. Testing began at 100 days, first with no hormone replacement, then with TP replacement, then again with no hormone replacement, and finally with EB. With TP in adulthood, both groups of males preferred females, but with EB in adulthood, only those that had received TP on Days 2 and 4 preferred females (Figure 1); the others preferred males. These results show that neonatally castrated males are feminized, but this feminization is expressed only following adult EB; TP can make up for the neonatal absence of testes; and early TP masculinizes females.

An experiment by de Jonge, Muntjewerff, Louwerse, and van de Poll (1988) compared the sexual orientation of female rats injected with TP within 24 h of birth with

Figure 1. Percentage of test time spent near stimulus males versus females by subject rats. Data shown are from females (F) injected with oil or testosterone propionate (TP) on Day 5 (Groups F-OIL-TP and F-TP-TP, respectively) and from males (M) castrated (CA) at 24–36 h after birth and given oil or TP on Days 2 and 4 (Groups M-CA-EB and M-CA+TP-EB, respectively). Females were ovariectomized before testing; data shown are from tests conducted following TP (female Groups F-OIL-TP and F-TP-TP) or estradiol benzoate (EB) treatment (male Groups M-CA-EB and M-CA+TP-EB). All preferences in either direction were statistically significant. (Data from "Sex-Specific Orientation in Female and Male Rats: Development and Effects of Early Endocrine Manipulation" by B. J. Meyerson, M. Eliasson, and J. Hetta (pp. 451–460). In A. M. Kaye and M. Kaye (Eds.), *Development of Responsiveness to Steroid Hormones: Advances in the Biosciences* (Vol. 25), 1980. Copyright 1980 by Pergamon Press. Used by permission.)

that of control females. One-third of each group was ovariectomized at 90 days, another third was ovariectomized at 30 days and given an E implant between 30 and 90 days of age, and the final third was ovariectomized at 30 days and sham implanted. All females were treated with TP from 104 to 125 days and then tested. All of the groups except those receiving neither early androgen nor pubertal E significantly preferred females (Figure 2); the two remaining groups were not different from each other, but were different from all the other groups. Thus, neonatal androgen induced orientation to female stimuli. In addition, pubertal E treatment appeared to have induced a preference for females. This may represent a very interesting kind of "late" organization. Alternatively, the effect might be experiential (de Jonge et al., 1988), for the females had been given tests for mounting immediately prior to the tests for sexual orientation, and such experience is known to modify female rat sexual preferences (de Jonge et al., 1987).

HAMSTERS (*Mesocricetus auratus*)

Little is known about the social organization of wild hamsters, but based on observations of laboratory-reared animals in seminatural environments, females are proba-

bly solitary and are quite aggressive toward males except during proestrus and early estrus (Lisk, Ciccio, & Caranzaro, 1983). Males seek out burrows of females and are permitted in the burrow if the female is proestrous. The pair is together for about a day before the female evicts the male from the burrow.

To determine if early castration changes the sexual preferences of male hamsters, Johnson and Tiefer (1972) used a modified T-maze apparatus with a stimulus female in heat in one goal box and an intact male in the other. The groups tested included intact males, males castrated on Day 1 or Day 60, and females ovariectomized on Day 60. Prior to testing, the intact males were injected with oil; half of each of the other groups was injected with TP, and the other half with EB plus P. The numbers of subjects were too small (4 per group per adult hormone treatment) for comparisons between groups to reach statistical significance, but nonetheless the results were clear enough to be interesting. Of the control groups, most of the intact and Day 60 castrated males injected with TP preferred females; Day 60 ovariectomized females injected with EB plus P all preferred males. Neither of the groups gonadectomized on Day 60 showed any preferences when injected with heterologous hormones (EB plus P for males, TP for females). The Day 1 castrated males preferred females if injected with TP but preferred males if injected with EB plus P.

Three points can be concluded from these results: hamsters receiving homologous hormone replacement show

Figure 2. Percentage of test time spent with stimulus males versus females by female subject rats. E = estradiol. See text for a description of the groups. All females were ovariectomized and receiving testosterone propionate at the time of testing. * $p < .05$, compared with nonandrogenized intact or sham control females, using female percentage minus male percentage as the measure. (Data from "Sexual behavior and sexual orientation of the female rat after hormonal treatment during various stages of development" by F. H. de Jonge, J.-W. Muntjewerff, A. L. Louwerse, and N. E. van de Poll, 1988, *Hormones & Behavior*, 22, pp. 100–115. Copyright 1988 by Academic Press. Used by permission.)

distinct opposite-sex preferences, making hamsters a good species for studying sexual preferences; heterologous hormones do not reveal these preferences, which means that adult hormone exposure influences sexual preferences; and early castration of males results in female-like preferences following adult treatment with female sex hormones, indicating that testicular hormones secreted between Day 1 and Day 60 are an important determinant of the normal male preference for females. However, early castration did not completely sex reverse the males; following adult TP, they still preferred females, rather than showing no preference as females given adult TP would do, implying that hormones prior to Day 1 or nonhormonal factors also shape later sexual preference.

FERRETS (*Mustela furo*)

Two experiments (Martin & Baum, 1986; Stockman, Callaghan, & Baum, 1985) have established the European ferret as a valuable species for studying hormonal influences on sexual preferences. Martin and Baum (1986) implanted females from the day of birth to Day 15 with T, 5- α -dihydrotestosterone (DHT; an androgenic metabolite of T), or E. Controls included females implanted with cholesterol or with empty capsules and unimplanted females. All subjects were gonadectomized at 11 weeks and tested without hormone replacement. Additional control unimplanted males and females were gonadectomized at 11 weeks and treated with T (males), E (some females), or E plus P (other females) before testing. Tests were conducted in a square arena with four stimulus animal compartments, and the time spent near each stimulus was recorded. Stimulus animals were two ovariectomized females brought into estrus with E implants, a castrated male, and an intact male implanted with T.

Control females not receiving adult hormone replacement spent more time near both kinds of males than near females, and control females receiving adult E or E plus P were no different. Control males without adult hormone replacement showed no preferences, but spent the same amount of time near all the stimulus animals; adult T changed this lack of preference to a preference for an estrous female stimulus. Thus, control ferrets show sexual preferences in this situation. With homologous hormone replacement females prefer males and males prefer females, whereas without replacement females still prefer males, but males show no preference. Early treatment with T masculinized the preferences of females, in that, like males, they showed no preference, but DHT had no effect on preferences (Figure 3). Early E-treated females preferred intact males and females about equally, but preferred castrated males to females, and thus fell in between early T-treated females and controls. What cannot be told from this experiment is whether early T-treated females given adult T would prefer females, as would be predicted.

Stockman et al. (1985) used a T-maze apparatus with two stimuli: a sexually active intact male and an ovariec-

Figure 3. Percentage of test time spent by female ferrets near stimulus males versus females. The three noncontrol groups were implanted with testosterone (T), 5- α -dihydrotestosterone (DHT), or estradiol (E) on the day of birth. Results shown are from females ovariectomized at 11 weeks who were not receiving hormone replacement at the time of testing. (Data from "Neonatal exposure of female ferrets to testosterone alters sociosexual preferences in adulthood" by J. T. Martin and M. T. Baum, 1986, *Psychoneuroendocrinology*, 11, 167-176. Copyright 1986 Pergamon Press. Used by permission.)

tomized female brought into estrus with an E implant. The following groups were tested: control males and females gonadectomized at 35 days, males castrated at 5 or 20 days, females gonadectomized at 5 days, and females gonadectomized at 5 days and given high- or low-dosage T implants either from 5 to 20 days or from 20 to 35 days. Animals were tested as adults following implantation with T and again following injection of EB. None of the groups showed any significant preferences for one sex or the other following adult T. (In Martin & Baum's, 1986, experiment, males given adult T preferred females; procedural differences are believed to account for this discrepancy [Stockman et al., 1985].) Following adult EB, control females preferred males and chose males more often than did any of the male groups, indicating that this preference for males is sexually differentiated (Figure 4). Males castrated on Day 5 chose males more often than males castrated at 20 days or control males castrated at 35 days, indicating that early castration feminizes the sexual preferences of males. Females implanted with the high T dose from 5 to 20 days chose males less often than control females, indicating that T during development masculinized sexual preference.

These results show that sexual preferences of ferrets result in part from the influences of sex hormones between 5 and 20 days after birth. The manipulations never completely reversed sexual preference (i.e., early castrated males did not choose like control females, and early T-treated females did not choose like control males), which could mean that prenatal as well as postnatal hormones

Figure 4. Percentage of trials in which stimulus males versus females were chosen by ferrets. Subjects were males (M) castrated at 5 (M-5), 20 (M-20), or 35 (M-35) days and females (F) ovariectomized at 5 (F-5) or 35 (F-35) days. Group F-5-T received a relatively high dose of testosterone from Days 5-20. Results shown are for tests following adult injection of estradiol benzoate. * $p < .05$ compared with same-sex controls (Group M-35 or F-35). (Data from "Effects of Neonatal Castration and Testosterone Propionate Treatment on Sexual Partner Preference in the Ferret" by E. R. Stockman, R. S. Callaghan, and M. J. Baum, 1985, *Physiology & Behavior*, 34, pp. 409-414. Copyright 1985 Pergamon Press. Used by permission.)

contribute to sexual preference in this species (Baum, Erskine, Stockman, & Lundell, 1985).

DOGS (*Canis familiaris*)

Domestication seems to have had a marked effect on the mating system of dogs. Wolves, the wild ancestors of dogs, form long-term monogamous pair bonds (Kleiman, 1977). In contrast, domestic dogs appear to mate somewhat promiscuously, although systematic observation suggests that mating is far from indiscriminate. Although free-ranging urban male dogs all attempt to mate with an estrous female, only some males are successful (Daniels, 1983), implying mate choice on the part of the female. Estrous female beagles strongly prefer to mate with some males rather than with others (Beach & LeBoeuf, 1967). Both wild and domestic dogs are relatively monomorphic.

Beach, Johnson, Anisko, and Dunbar (1977) tested females that had been treated with T *in utero*, in infancy, or during both periods. A stimulus male or estrous female was tethered in the center of a circular outdoor arena, and the total time spent "visiting" the stimulus was recorded. All females, including untreated controls, were

ovariectomized as adults and were tested during two periods: first with a stimulus male after receiving EB, then again with a stimulus estrous female after receiving TP. Controls spent more time with males (after EB) than with females (after TP), but all three early androgenized groups spent more time with females than with males, suggesting a reversal of sexual orientation (Figure 5). This reversal was greatest with combined pre- and postnatal T treatment.

Strictly speaking, this is not a design that allows direct conclusions to be drawn about sexual orientation, because adult sex hormone treatment varied with stimulus sex and the two stimulus sexes were presented at rather different times, producing possible order effects. However, the results suggest that pre- and postnatal T might be important for the differentiation of sexual preference in dogs, and that further research on this species is highly desirable.

PIGS (*Sus scrofa*)

The basic unit of social organization of wild pigs in Europe is a small group of females with their young (Frädrich, 1974; Gründlach, 1968). Males are allowed near the group only during the breeding season. Estrous

Figure 5. Time spent in a 600-sec test visiting a tethered stimulus dog. The three noncontrol groups were treated with T (testosterone) in infancy (I), in utero (U), or during both periods (U+I). As adults subjects were ovariectomized and given either estradiol benzoate (tests with stimulus males) or testosterone propionate (tests with stimulus females). (Data from "Hormonal Control of Sexual Attraction in Pseudohermaphroditic Female Dogs" by F. A. Beach, A. I. Johnson, J. J. Anisko, and I. F. Dunbar, 1977, *Journal of Comparative & Physiological Psychology*, 91, pp. 711-715. Copyright 1977 American Psychological Association. Used by permission.)

females probably mate with more than one male, and males mate with more than one female; pair bonds are unlikely. Wild pigs are much more dimorphic physically than rodents or dogs. Wild and domestic pigs of both sexes engage in courtship or proceptive behavior before copulating (Signoret, 1970).

The sexual preferences of pigs have been systematically investigated by Signoret (1970). In choice tests conducted in large modified T-mazes with intact male versus nonestrous female stimuli, males show no consistent preference and spend relatively little time with either stimulus. Nor do males markedly prefer estrous to nonestrous females. Nonestrous females behave quite similarly. However, estrous females or ovariectomized females given a single EB injection show a marked preference for the male, spending most of the test standing near him. This seems to be a sexual preference, rather than a general social preference, because while standing near the male the female adopts the receptive posture seen during copulation—immobilization with the ears cocked. Males castrated as adults and given an EB injection do not show this behavior and do not spend time with males in choice tests. Thus in this species, females, but not males, show a distinct highly estrogen-dependent sexual preference in choice tests.

Two experiments have shown that this difference between males and females in these choice tests is a result of sex hormone influences earlier in development. To understand these experiments, it is important to know that the pig seems to be an exception to the usual rule that organizational hormone effects occur only early in development. Anatomical sexual differentiation is complete before birth (Elsaesser, 1982), as is typical of highly precocial animals, yet castration of males as late as 4 months after birth (early puberty) can produce long-lasting (permanent?) feminization of copulatory behavior (Berry & Signoret, 1984; Ford, 1982). T treatment given from 3 to 6 months to males castrated shortly after birth produces long-lasting defeminization (Ford & Christenson, 1987).

In an experiment by Ford (1983a), males were castrated within 48 h of birth, at age 4 months, or at 8 months (controls). Female controls were ovariectomized at 8 months. Beginning at 12 months, pigs were injected with EB and tested biweekly in a modified T-maze with intact male versus ovariectomized female stimuli. The dose of EB was then increased for a second trial because it seemed to be insufficient. Figure 6 shows the results from the second trial. Males castrated shortly after birth were quite feminized and, like the control females, they spent much time near the stimulus male. Males castrated at 4 or 8 months spent less time with the male and more time with the female; they showed no preference.

Based on the results of this experiment, females or early-castrated males treated with sex steroids postnatally should be masculinized and should not prefer males. The effect of androgen treatment during development on sex-

Figure 6. Time spent by pigs in the stimulus male versus female end of a T-maze during two 5-min tests. Male (M) and female (F) subjects were gonadectomized 48 h or less after birth (M-48) or at age 4 (M-4) or 8 (F-8 and M-8) months; all subjects were injected with estradiol benzoate before testing. * $p < .05$ compared with M-4 or M-8. (Data from "Postnatal Differentiation of Sexual Preference in Male Pigs" by J. J. Ford, 1983a, *Hormones & Behavior*, 17, pp. 152-162. Copyright 1983 Academic Press. Used by permission.)

ual orientation has not yet been studied in pigs. However, male pigs, even juveniles, produce very large amounts (more than 40 pg/ml) of estrogens, such as estradiol, as well as androgens (Ford, 1983b). Does estradiol defeminize sexual orientation during juvenile development in this species? This question has been addressed in an experiment (Adkins-Regan, Orgeur, & Signoret, 1988) in which the following groups were tested: control females ovariectomized at 2 months, females ovariectomized at 2 months and implanted with EB from 3 to 5.5 months, control males castrated at 5.5 months, males castrated at 2 weeks, and males castrated at 2 weeks and implanted with EB from 3 to 5.5 months. Beginning at age 6.5 months, each subject was injected with EB and given T-maze choice tests. The results are shown in Figure 7. As expected on the basis of Ford's (1983a) experiment, males castrated late were uninterested in stimulus males, and males castrated at 2 weeks resembled control females by orienting to the male stimulus. As hypothesized, the EB implants masculinized the sexual orientation of both females and early-castrated males.

The results of these experiments in pigs suggest the following conclusions for this species: sexual orientation is sexually differentiated, testicular hormones produced during development are an important determinant of these sexual preferences, hormonal organization of sexual preference is possible surprisingly late in development, and estradiol may be involved in the differentiation of male sexual orientation.

Figure 7. Time spent by pigs near the male barrier minus time spent near the female barrier during 5-min choice tests. M-IN are males castrated at 5.5 months (and thus intact during development); all other groups were gonadectomized at 2 months (females) or 2 weeks (males). M-EB and F-EB were implanted with estradiol benzoate (EB) from 3 to 5.5 months. All subjects were injected with EB prior to testing. * $p < .05$ compared with same-sex controls (M-CA or F-OV). (Data from "Sexual Differentiation of Reproductive Behavior in Pigs: Defeminizing Effects of Pubertal Estradiol" by E. Adkins-Regan, P. Orgeur, and J. P. Signoret, 1988 (manuscript submitted for publication).

ZEBRA FINCHES (*Poephila guttata*)

The behavior and social organization of zebra finches are very similar in both field and laboratory (Immelmann, 1967). The birds nest colonially, are sexually dimorphic in plumage and beak color, and form long-term monogamous pair bonds, although extrapair copulations are occasionally seen in the laboratory. Both sexes appear to take an active role in mate selection. Birds that are paired clearly indicate their status to human observers by several behaviors, such as spending a great deal of time in physical contact with each other, preening each other, building a nest together, and being in a nest box together (Butterfield, 1970). Copulation itself is relatively infrequent.

In the laboratory, most finches pair with an opposite-sex partner. In a recent experiment (Adkins-Regan & Ascenzi, 1987), male and female zebra finches were injected with EB during the first 2 weeks after hatching. Controls were injected with the vehicle. After reaching puberty, the birds were gonadectomized, implanted with TP, and tested for sexual and other social behavior. The testing procedure included introducing each subject into

a colony cage containing breeding pairs and unpaired birds of both sexes, and observing the subject daily. The early EB treatment had no effect on the pairing choices of the males, but it masculinized the preferences of the females. Some of these early EB-treated females actually succeeded in pairing with other females, mainly by preventing the target females from being able to pair with males.

All the subjects in this experiment were reared in unisex cages. Although the early EB treatment itself clearly changed the sexual orientation of EB-treated females (the control females were also raised in unisex cages, yet preferred males), it is possible that it has this effect only if the finches also experience unisex rearing.

MACAQUE MONKEYS (*Macaca spp.*)

The various species of macaques live in groups consisting of females and their young together with several adult males (Melnick & Pearl, 1986; Richard, 1985). Females remain in their natal troop, whereas males disperse before adulthood; females usually mate with males who have emigrated into the troop, but occasionally with extratroup males (Smuts, 1986). Dominance interactions among the males play an important role in determining who gets to mate with a given female.

Homosexual interactions have been observed in many species of wild and captive primates (for references, see Akers & Conaway, 1979; Chevalier-Skolnikoff, 1976) and have been described in detail in two species of macaques. In a heterosexual group of rhesus macaques (*Macaca mulatta*) housed in an outdoor corral, 7 out of 8 of the females mounted other females extensively (Akers & Conaway, 1979). Although the mounter was usually the more dominant of the 2 females, the behavior itself seemed much more sexual than agonistic; its duration and pronounced genital focus clearly distinguished it from the brief mounts that serve a dominance function in this species. Homosexual mounting, like heterosexual mounting, varied as a function of menstrual cycle stage; females were mounted most frequently during the periovulatory period and least frequently during the luteal phase. Sometimes the females appeared to prefer females to males as sexual partners; it would be interesting to see if females' preferences for other females over males as partners depends on cycle stages.

Chevalier-Skolnikoff (1976) described sexual interactions between males and between females in heterosexual groups of stump-tailed macaques (*Macaca arctoides*). Male-male and female-female interactions were very similar. As in the rhesus macaque observations described above, the behavior did not occur in aggressive contexts, although who mounted versus who was mounted could sometimes be predicted by knowing dominance status. Instead, the behavior occurred mainly between animals with strong affectional ties. Heterosexual mating in this species is much more independent of female cycle stage than in rhesus macaques, and female-female sexual interactions were similarly independent, implying minimal if any hormonal control.

Thus, endocrinologically normal macaques are capable of initiating and participating in sexual interactions with either sex, as if sexual preferences and behavior are not highly sexually differentiated. Furthermore, engaging in homosexual interactions does not necessarily imply a homosexual orientation, which would require consistent preferences for homosexual over heterosexual activity, even when both are possible.

Can early hormone exposure lead to such preferences? There are no experiments in which hormones have been manipulated early in development and sexual preferences have been assessed in choice tests in adulthood. The most relevant information comes from an experiment (Pomerantz, Roy, Thornton, & Goy, 1985) in which proceptive behavior toward a tethered adult male was measured in anatomically masculinized rhesus females born to mothers treated with TP or DHTP, in males castrated shortly after birth, and in control females. The females were left gonadally intact, and all groups were given an estradiol implant prior to testing. For all four measures of proceptive behavior, the males had lower scores than the control females, indicating that these behaviors are in fact sexually differentiated in this species. For three of the four proceptivity measures, the early androgenized females scored lower than control females; for two of these their scores fell between control females and early castrated males, and for the third measure (solicits per minute) they were completely defeminized. These results suggest a possible effect of early androgen exposure on sexual orientation in female rhesus monkeys, but additional research with both male and female stimuli would be necessary to distinguish between a change in sexual orientation and a reduction in sexual motivation.

HUMANS (*Homo sapiens*)

Obviously, we cannot expect to find human studies exactly comparable to these animal experiments, but comparing people with certain endocrine disorders or medical treatments with controls matched on other dimensions can reveal whether excesses or deficiencies of sex hormones during early development might change sexual orientation. Anatomical differentiation takes place prenatally in humans, and it has been hypothesized that exposure to excess androgens during fetal life produces women that prefer other women as partners, and that abnormally low androgen produces men that prefer other men (Dörner, 1988). The effect of prenatal exposure to excess estrogen in men or women is harder to predict. If estrogens mimic androgens in humans as they do in many mammals (Feder, 1981; Goy & McEwen, 1980), then they should masculinize women and have little effect in men; however, if they do not or if they interfere with the actions of endogenous androgens, they might feminize males and have little effect on females.

Ehrhardt and Meyer-Bahlburg (1981) reviewed many of the classic studies of people prenatally exposed to abnormal levels of sex hormones to see if any effect on sexual orientation had been noticed. Some studies were in-

conclusive either because there were no controls or because the subjects were too young to have a well-developed erotic life. Some examined people exposed to abnormal hormone levels in adulthood as well as prenatally, and thus are quite confounded in terms of testing a prenatal hormone hypothesis. Others found no difference between exposed and control subjects.

Four studies done since Ehrhardt and Meyer-Bahlburg's (1981) review have directly addressed the prenatal hormone hypothesis. All four assessed sexual orientation by gathering information in interviews about sexual fantasies, erotic imagery, and overt sexual behavior.

Two of these studies examined people whose mothers had been treated with the synthetic estrogen diethylstilbestrol (DES) during pregnancy. Kester, Green, Finch, and Williams (1980) found no difference in the incidence of homosexual behavior between control men and men exposed prenatally to DES, progesterone, or DES plus progesterone. The controls were not as well matched, however, as is desirable in this kind of research. Ehrhardt et al. (1985) interviewed DES-exposed 17- to 30-year-old women. Controls were non-DES-exposed women from the same clinic who had abnormal Pap smears or, when possible, the subjects' own sisters, who are excellent controls for this kind of research. Kinsey rating scales were used to compare the DES and control women. The former had higher scores (indicating more bisexuality or homosexuality) for most comparisons. Of 10 comparisons, 6 were significant when the controls were unrelated women, and 2 were significant when the controls were sisters. The authors present several arguments in favor of a hormonal explanation for the results, but point out that this hormonal influence is relatively minor; only 1 of the 30 DES women had been nearly exclusively homosexual throughout her sexual life. They also point out that because DES women sometimes have abnormal adult hormone levels, the data do not distinguish between an adult and a prenatal hormone hypothesis.

Of the two other recent studies, one is a follow-up of 12 women aged 16-27 who had been exposed to anatomically masculinizing progestins before birth (Money & Matthews, 1982). Information relevant to sexual orientation was available for only 6: 1 had had no erotic experience, whereas the other 5 were exclusively heterosexual. Finally, Money, Schwartz, and Lewis (1984) interviewed a group of women over 17 years of age who had congenital virilizing adrenal hyperplasia (CVAH), a genetic disorder in which the adrenals produce excess androgen and insufficient corticosteroids. If treated shortly after birth, as was the case for these subjects, such individuals are exposed to abnormally high levels of androgens prenatally but not postnatally. When compared with women with two different disorders of sexual differentiation, neither involving excess androgen, CVAH women were more likely to have had homosexual imagery and experience. Unfortunately, medically normal controls were not included in the study.

Thus, of these four recent studies, two obtained positive results in support of a prenatal hormone hypothesis

of sexual orientation, but one of these two did not include any normal controls. Furthermore, as Ehrhardt et al. (1985) cautioned, observations of people who have medical abnormalities (and who know they do) may not be relevant to the problem of explaining sexual orientation in people without such abnormalities.

One naturally occurring disorder of sexual differentiation is particularly interesting in this context. Genetic males with 5-alpha-reductase deficiency have abnormally low levels of DHT and are quite female-like in anatomical appearance until puberty, at which point marked physical masculinization occurs (Imperato-McGinley, Peterson, Gautier, & Sturla, 1979). Many of these individuals that have grown up as girls subsequently live as men, including some that have been married at a young age to men, and have later married women (Herdt & Davidson, 1988). These observations suggest considerable lability in sexual orientation, but do not tell us whether this lability is possible because the individuals who changed had been exposed prenatally to testosterone (Imperato-McGinley et al., 1979) or because of sociocultural factors such as higher societal status for men (Herdt & Davidson, 1988).

DISCUSSION

These experiments have established that in laboratory tests, both sexes of rats, hamsters, and finches exhibit clear heterosexual orientation, in that they prefer to spend time or pair with the opposite sex. Female pigs and ferrets prefer males, whereas males show no reliable preferences for either sex. In rats, hamsters, ferrets, and pigs, these sexual preferences have been shown to be dependent on adult activational hormones, in that they are reduced by gonadectomy or are different in gonadectomized animals receiving homologous and those receiving heterologous hormones.

Table 1 summarizes the effect of pre- or early postnatal hormone manipulations on the sexual preferences of animals. In each of these species, either early castration of males or early T treatment of females or both have been found to partially or completely sex reverse sexual orientation. It is possible to conclude that in several species

of mammals and birds, sex hormones produced during neonatal or juvenile (pigs) development are an important determinant of adult sexual orientation. Analogous experiments with macaques and humans are suggestive of a similar effect but are not yet conclusive. Conspicuously absent from Table 1 are any studies of mammals with monogamous mating systems or pair bonds (although wolves, the wild ancestors of domestic dogs, are monogamous). Table 1 also reveals that the total number of experiments on hormonal organization of sexual orientation in animals is surprisingly small.

Comparisons with the Organization of Copulatory Behavior

Most of the results summarized in Table 1 are similar to the well-known organizing effects of early sex steroids on copulatory behavior *per se*, in that the effects are long lasting or permanent, are produced by steroid hormone actions relatively early in development, and result in behavioral sex reversal such that early castrated males are feminized and early T-treated females are masculinized. But how far does this parallel extend? Are there any important differences between sexual orientation and copulation with respect to the role of hormones in differentiation, or are they merely two reflections of the same underlying process?

One way to approach this question is to examine whether descriptions of species differences in the organization of copulation fit sexual orientation as well. Descriptions that include birds do reveal a major discrepancy between the differentiation of copulation and sexual orientation. In quail, chickens, and zebra finches, early sex hormone exposure causes demasculinization of copulation (it makes males female-like by decreasing male-typical copulation) rather than masculinization or defeminization (Adkins-Regan, 1987). In zebra finches, E treatment masculinized sexual preference in females, rather than demasculinizing it in males, and did so without masculinizing the copulatory behavior of the females (Adkins-Regan & Ascenzi, 1987).

Another way to compare early hormone effects on sexual orientation with its effects on copulatory behavior is to consider the timing of the critical periods for sex rever-

Table 1
Summary: Hormones and Sexual Orientation

Species	Effect of Early Castration on Males	Effect of Neonatal T or E Treatment on Females	References
Rat	Complete feminization	Masculinization (T)	de Jonge et al., 1988 Eliasson & Meyerson, 1981 Meyerson et al., 1980
Hamster	Feminization	Not yet known	Johnson & Tiefer, 1972
Ferret	Partial feminization	Partial masculinization (T)	Martin & Baum, 1986 Stockman et al., 1985
Dog	Not yet known	Complete masculinization (T)?*	Beach et al., 1977
Pig	Complete feminization	Complete masculinization (E)†	Ford, 1983a
Zebra finch	Not yet known	Masculinization (E)	Adkins-Regan & Ascenzi, 1987

Note—T = testosterone, E = estradiol. Feminization refers to decreased preference for females and/or increased preference for males. Masculinization refers to decreased preference for males and/or increased preference for females. *The preferences of males were not measured; see also discussion in text of the experimental design. †Treatment given from 3 to 5.5 months (early puberty).

sal. The clearest example of a difference between the two critical periods can be seen in the pig. Males castrated at 4 months were receptive when mounted by stimulus males but did not prefer males in the choice tests (Ford, 1983a). Thus masculinization of sexual preference by testicular hormones was already complete at 4 months, but defeminization of receptivity was not; the critical period ends at different times for these two behaviors.

In several mammals, early T masculinizes or defeminizes copulatory behavior via conversion to estrogenic metabolites (aromatization), and E itself mimics the effect of T (Feder, 1981; Goy & McEwen, 1980). Does sexual orientation share the same pattern of steroid specificity? The results of Martin and Baum's (1986) experiment are equivocal with respect to an aromatization hypothesis, because while DHT, which cannot be aromatized, failed to masculinize the sexual preferences of female ferrets, E was only partially effective. E strongly masculinized sexual preference in pigs (Adkins-Regan et al., 1988), but the effect of T on the sexual orientation of this species has not yet been determined.

Thus experiments on finches and pigs make it clear that sex hormones acting during development can change sexual orientation independently of copulation: these are separate categories of behavior. Whether sexual orientation can also be dissociated from courtship or proceptive behavior by early hormone manipulations remains to be seen.

Animal Models of Sexual Orientation

Each of the species that has been used has advantages and disadvantages as a model for sexual orientation research. The fact that both sexes show significant sexual preferences, but in opposite directions, makes rats, hamsters, and zebra finches good choices. The fact that little is known about the mating system of wild ferrets (or, for that matter, rats and hamsters) is a problem. Pigs have the advantages of obvious physical dimorphism and easily measured very clear female preferences for males that are activated by E alone rather than E plus P (Signoret, 1970). Zebra finches offer distinctive plumage dimorphism, pronounced pair bond behavior, and a monogamous mating system in which both sexes appear to actively choose a mate. Depending on whether the researcher wishes to emphasize or deemphasize the genital component of sexuality, pigs (in which sexual orientation can be reversed without altering the genitalia) and zebra finches (who have no external genitalia) are either foolish or wise choices.

Are any of these species suitable models for understanding human sexual orientation? It may well be that for all of the nonprimates, the best answer is no; because of the profound cognitive and emotional components of the human phenomenon, sexual orientation in nonprimates and humans is simply not homologous (Beach, 1979; Davidson, 1979; Gooren, 1984; Meyer-Bahlburg, 1984). Primates have the potential to be particularly good models for human sexual behavior, both because of phylogenetic relatedness and because, in contrast to most other mam-

mals, sexual behavior can occur outside of the periovulatory period, suggesting that sexual behavior has social/affective functions other than reproduction in the strict sense. It is unfortunate, therefore, that there have been very few studies of sexual orientation in any nonhuman primates.

Meyer-Bahlburg (1984) provided two additional reasons why it is difficult to apply animal models to the human situation, both of which deserve reevaluation. First, humans can have homosexual preferences without having to receive heterologous hormones in adulthood; the adult sex hormone levels of homosexuals are normal for their biological sex. Viewed in this way, it could be argued that animal experiments in which the early treated animals are left intact, although quite confounded if the purpose is testing any organizational theory of sexual orientation, are actually preferable if the goal is models for human homosexuality. However, the experiments reviewed here show that even in animals, reversal of sexual orientation does not necessarily require heterologous hormones in adulthood. In the Meyerson et al. (1980) experiment, neonatally androgenized female rats were masculinized when tested following either EB or TP in adulthood, and in the Adkins-Regan and Ascenzi (1987) experiment, neonatally EB-treated female finches preferred female partners regardless of whether they received EB or TP as adults.

Meyer-Bahlburg's (1984) second point was that in the animal experiments, the individuals are anatomically as well as behaviorally sex reversed, whereas human homosexuals are anatomically normal. In pigs, however, complete reversal of sexual orientation has been obtained without any alteration in sexual anatomy (Ford, 1983a).

The Psychobiology of Sexual Orientation

The value of research is not, however, a simple function of its usefulness with respect to understanding humans. Regardless of whether these animal experiments shed any light on our species, they are an important first step for understanding the biology of sexual orientation in the animal kingdom. Our failure to understand the origins of sexual preferences in humans is matched by our ignorance of them in animals. The sexual orientation dimension of mate choice has been neglected even by the many animal behaviorists interested in mate choice, who have instead focused on decisions about with which species to mate or with which individual from among opposite sex conspecifics to mate (Bateson, 1983).

Such understanding will require more than simply experiments on effects of early hormones. Also important will be studies of the role of the social environment during development, which is known to be important for species mating preferences (Bateson, 1978), and possible interactions between that environment and hormones (see Meaney, 1988; Moore, 1984). The developmental determinants of sexual orientation might well be different in different species in ways that can be predicted from the mating system and social organization. For example, there may be more developmental constraints on sexual prefer-

ences in monogamous species, for which a "mistake" would be particularly costly, or in females, who are expected to be "choosier" about selecting a mate (Daly & Wilson, 1983). Marine animals that congregate in groups and release gametes into the water might not have any sexual preferences at all.

Finally, a broad psychobiological approach to sexual orientation should include greater attention to this dimension of sexuality in wild animals studied in the field (Conover & Hunt, 1984; Wingfield, Newman, Hunt, & Farner, 1982). A report by Jamieson and Craig (1987) provides a particularly fascinating illustration. During 3 years of observations of communally breeding pukekos (*Porphyrio porphyrio*, birds native to New Zealand), the authors witnessed 555 instances of heterosexual courtship/copulation interactions, and 41 homosexual interactions (12 male-male and 29 female-female), some of which resulted in cloacal contact. Most of the female-female copulations occurred during the period of egg laying. It is tempting to hypothesize that they serve some physiological function, as has been shown for female-female matings in a unisexual lizard species (Crews, 1987).

REFERENCES

- ADKINS-REGAN, E. (1981). Early organizational effects of hormones: An evolutionary perspective. In N. T. Adler (Ed.), *Neuroendocrinology of reproduction: Physiology and behavior* (pp. 159-228). New York: Plenum Press.
- ADKINS-REGAN, E. (1987). Sexual differentiation in birds. *Trends in Neurosciences*, **10**, 517-522.
- ADKINS-REGAN, E., & ASCENZI, M. (1987). Social and sexual behaviour of male and female zebra finches treated with oestradiol during the nestling period. *Animal Behaviour*, **35**, 1100-1112.
- ADKINS-REGAN, E., ORGEUR, P., & SIGNORET, J. P. (1988). *Sexual differentiation of reproductive behavior in pigs: Defeminizing effects of pubertal estradiol*. Manuscript submitted for publication.
- AKERS, J. S., & CONAWAY, C. H. (1979). Female homosexual behavior in *Macaca mulatta*. *Archives of Sexual Behavior*, **8**, 63-80.
- BATESON, P. P. G. (1978). Early experience and sexual preferences. In J. B. Hutchison (Ed.), *Biological determinants of sexual behaviour* (pp. 29-54). Chichester, England: Wiley.
- BATESON, P. P. G. (Ed.). (1983). *Mate choice*. Cambridge, England: Cambridge University Press.
- BAUM, M. J. (1979). Differentiation of coital behavior in mammals: A comparative analysis. *Neuroscience & Biobehavioral Reviews*, **3**, 265-284.
- BAUM, M. J., CARROLL, R. S., ERSKINE, M. S., & TOBET, S. A. (1985). Neuroendocrine response to estrogen and sexual orientation. *Science*, **230**, 960-961.
- BAUM, M. J., ERSKINE, M. S., STOCKMAN, E. R., & LUNDELL, L. A. (1985). Endocrine control of behavioural sexual differentiation in the male ferret. In R. Gilles & J. Balthazart (Eds.), *Neurobiology* (pp. 142-148). Berlin: Springer-Verlag.
- BEACH, F. A. (1979). Animal models for human sexuality. In *Sex, Hormones and Behaviour* (Ciba Foundation Symposium 62, new series, pp. 113-132). Amsterdam: Excerpta Medica.
- BEACH, F. A., JOHNSON, A. I., ANISKO, J. J., & DUNBAR, I. F. (1977). Hormonal control of sexual attraction in pseudohermaphroditic female dogs. *Journal of Comparative & Physiological Psychology*, **91**, 711-715.
- BEACH, F. A., & LEBOEUF, B. J. (1967). Coital behaviour in dogs: I. Preferential mating in the bitch. *Animal Behaviour*, **15**, 546-558.
- BERRY, M., & SIGNORET, J.-P. (1984). Sex play and behavioural sexualization in the pig. *Reproduction, Nutrition et Développement*, **24**, 507-513.
- BUTTERFIELD, P. A. (1970). The pair bond in the zebra finch. In J. H. Crook (Ed.), *Social behaviour in birds and mammals* (pp. 249-278). London: Academic Press.
- CARR, W. J., LOEB, L. S., & DISSINGER, M. L. (1965). Responses of rats to sex odors. *Journal of Comparative & Physiological Psychology*, **59**, 370-377.
- CHEVALIER-SKOLNIKOFF, S. (1976). Homosexual behavior in a laboratory group of stump-tail monkeys (*Macaca arctoides*): Forms, contexts, and possible social functions. *Archives of Sexual Behavior*, **5**, 511-527.
- CONOVER, M. R., & HUNT, G. L. (1984). Experimental evidence that female-female pairs in gulls result from shortages of breeding males. *Condor*, **86**, 472-476.
- CREWS, D. (1987). Diversity and evolution of behavioral controlling mechanisms. In D. Crews (Ed.), *Psychobiology of reproductive behavior: An evolutionary perspective* (pp. 88-119). Englewood Cliffs: Prentice-Hall.
- DALY, M., & WILSON, M. (1983). *Sex, evolution and behavior* (2nd ed.). Boston: PWS.
- DANIELS, T. J. (1983). The social organization of free-ranging urban dogs: II. Estrous groups and the mating system. *Applied Animal Ethology*, **10**, 365-373.
- DAVIDSON, J. M. (1979). Biological determinants of sex: their scope and limitations. In H. A. Katchadourian (Ed.), *Human sexuality* (pp. 134-149). Berkeley: University of California Press.
- DE JONGE, F. H., BURGER, J., VAN HAAREN, F., OVERDIJK, H., & VAN DE POLL, N. E. (1987). Sexual experience and preference for males or females in the female rat. *Behavioral & Neural Biology*, **47**, 369-383.
- DE JONGE, F. H., EERLAND, E. M. J., & VAN DE POLL, N. E. (1986). The influence of estrogen, testosterone, and progesterone on partner preference, receptivity and proceptivity. *Physiology & Behavior*, **37**, 885-892.
- DE JONGE, F. H., KALVERDIJK, E. H., & VAN DE POLL, N. E. (1986). Androgens are specifically implicated in female rat sexual motivation. The influence of methyltrienelone (R1881) on sexual orientation. *Pharmacology Biochemistry & Behavior*, **24**, 285-289.
- DE JONGE, F. H., MUNTJEWERFF, J. -W., LOUWERSE, A. L., & VAN DE POLL, N. E. (1988). Sexual behavior and sexual orientation of the female rat after hormonal treatment during various stages of development. *Hormones & Behavior*, **22**, 100-115.
- DÖRNER, G. (1976). *Hormones and brain differentiation*. Amsterdam: Elsevier.
- DÖRNER, G. (1988). Neuroendocrine response to estrogen and brain differentiation in heterosexuals, homosexuals, and transsexuals. *Archives of Sexual Behavior*, **17**, 57-75.
- DUDLEY, C. A., & MOSS, R. L. (1985). LHRH and mating behavior: Sexual receptivity versus sexual preference. *Pharmacology Biochemistry & Behavior*, **22**, 967-972.
- EHRHARDT, A. A., & MEYER-BAHLBURG, H. F. L. (1981). Effects of prenatal sex hormones on gender-related behavior. *Science*, **211**, 1312-1318.
- EHRHARDT, A. A., MEYER-BAHLBURG, H. F. L., ROSEN, L. R., FELDMAN, J. F., VERIDIANO, N. P., ZIMMERMAN, I., & McEWEN, B. S. (1985). Sexual orientation after prenatal exposure to exogenous estrogen. *Archives of Sexual Behavior*, **14**, 57-77.
- ELIASSON, M., & MEYERSON, B. (1981). Development of sociosexual approach behavior in male laboratory rats. *Journal of Comparative & Physiological Psychology*, **95**, 160-165.
- ELLIS, L., & AMES, M. A. (1987). Neurohormonal functioning and sexual orientation: A theory of homosexuality-heterosexuality. *Psychological Bulletin*, **101**, 233-258.
- ELSAESSER, F. (1982). Endocrine control of sexual maturation in the female pig and sexual differentiation of the stimulatory oestrogen feedback mechanism. In D. J. A. Cole & G. R. Foxcroft (Eds.), *Control of Pig Reproduction* (pp. 93-116). London: Butterworth Scientific.
- FEDER, H. H. (1981). Perinatal hormones and their role in the development of sexually dimorphic behaviors. In N. T. Adler (Ed.), *Neuroendocrinology of reproduction: Physiology and behavior* (pp. 127-158). New York: Plenum Press.
- FORD, J. J. (1982). Testicular control of defeminization in male pigs. *Biology of Reproduction*, **27**, 425-430.

- FORD, J. J. (1983a). Postnatal differentiation of sexual preference in male pigs. *Hormones & Behavior*, **17**, 152-162.
- FORD, J. J. (1983b). Serum estrogen concentrations during postnatal development in male pigs. *Proceedings of the Society for Experimental Biology & Medicine*, **174**, 160-164.
- FORD, J. J., & CHRISTENSON, R. K. (1987). Influences of pre- and postnatal testosterone treatment on defeminization of sexual receptivity in pigs. *Biology of Reproduction*, **36**, 581-587.
- FRÄDRICH, H. (1974). A comparison of behaviour in the Suidae. In V. Geist & F. Walther (Eds.), *The behaviour of ungulates and its relation to management* (Vol. 1, pp. 133-143). Morges, Switzerland: IUCN.
- GLADUE, B. A., GREEN, R., & HALLMAN, R. E. (1984). Neuroendocrine response to estrogen and sexual orientation. *Science*, **225**, 1496-1500.
- GOOREN, L. J. G. (1984). Sexual dimorphism and transsexuality: Clinical observations. In G. J. De Vries, J. P. C. De Bruin, H. B. M. Uylings, & M. A. Corner (Eds.), *Sex differences in the brain: Progress in brain research* (Vol. 61, pp. 399-406). Amsterdam: Elsevier.
- GOOREN, L. (1986). The neuroendocrine response of luteinizing hormone to estrogen administration in heterosexual, homosexual, and transsexual subjects. *Journal of Clinical Endocrinology & Metabolism*, **63**, 583-588.
- GOOREN, L. J. G., RAO, B. R., VAN KESSEL, H., & HARMSEN-LOUMAN, W. (1984). Estrogen positive feedback on LH secretion in transsexuality. *Psychoneuroendocrinology*, **9**, 249-260.
- GOY, R. W., & McEWEN, B. S. (1980). *Sexual differentiation of the brain*. Cambridge, MA: MIT Press.
- GRÜNDLACH, H. (1968). Brutfürsorge, Brutpflege, Verhaltensontogenese und Tagesperiodik beim Europäischen Wildschwein (*Sus scrofa* L.). *Zeitschrift für Tierpsychologie*, **25**, 955-995.
- HERDT, G. H., & DAVIDSON, J. (1988). The Sambia "turn-in-man": Sociocultural and clinical aspects of gender formation in male pseudohermaphrodites with 5-alpha-reductase deficiency in Papua New Guinea. *Archives of Sexual Behavior*, **17**, 33-56.
- HETTA, J., & MEYERSON, B. J. (1978). Sexual motivation in the male rat: A methodological study of sex-specific orientation and the effects of gonadal hormones. *Acta Physiologica Scandinavica* (Suppl. 453), 1-68.
- IMMELMANN, K. (1967). *Australian finches in bush and aviary*. Sydney: Angus and Robertson.
- IMPERATO-MCGINLEY, J., PETERSON, R. E., GAUTIER, T., & STURLA, E. (1979). Male pseudohermaphroditism secondary to 5 α -reductase deficiency—a model for the role of androgens in both the development of the male phenotype and the evolution of a male gender identity. *Journal of Steroid Biochemistry*, **11**, 637-645.
- JAMIESON, I. G., & CRAIG, J. L. (1987). Male-male and female-female courtship and copulation behaviour in a communally breeding bird. *Animal Behaviour*, **35**, 1251-1253.
- JOHNSON, W. A., & TIEFER, L. (1972). Sexual preferences in neonatally castrated male golden hamsters. *Physiology & Behavior*, **9**, 213-218.
- KESTER, P., GREEN, R., FINCH, S. J., & WILLIAMS, K. (1980). Prenatal 'female hormone' administration and psychosexual development in human males. *Psychoneuroendocrinology*, **5**, 269-286.
- KLEIMAN, D. G. (1977). Monogamy in mammals. *Quarterly Review of Biology*, **52**, 39-69.
- LISK, R. D., CIACCIO, L. A., & CARANZARO, C. (1983). Mating behaviour of the golden hamster under seminatural conditions. *Animal Behaviour*, **31**, 659-666.
- MARTIN, J. T., & BAUM, M. T. (1986). Neonatal exposure of female ferrets to testosterone alters sociosexual preferences in adulthood. *Psychoneuroendocrinology*, **11**, 167-176.
- MCCLINTOCK, M. K. (1987). A functional approach to the behavioral endocrinology of rodents. In D. Crews (Ed.), *Psychobiology of reproductive behavior: An evolutionary perspective* (pp. 176-203). Englewood Cliffs, NJ: Prentice Hall.
- MEANEY, M. J. (1988). The sexual differentiation of social play. *Trends in Neurosciences*, **11**, 54-57.
- MELNICK, D. J., & PEARL, M. C. (1986). Cercopithecines in multi-male groups: Genetic diversity and population structure. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 121-134). Chicago: University of Chicago Press.
- MEYER-BAHLBURG, H. F. L. (1984). Psychoendocrine research on sexual orientation. Current status and future options. In G. J. De Vries, J. P. C. De Bruin, H. B. M. Uylings, & M. A. Corner (Eds.), *Sex differences in the brain: Progress in brain research* (Vol. 61, pp. 375-398). Amsterdam: Elsevier.
- MEYERSON, B. J., ELIASSON, M., & HETTA, J. (1980). Sex-specific orientation in female and male rats: Development and effects of early endocrine manipulation. In A. M. Kaye & M. Kaye (Eds.), *Development of responsiveness to steroid hormones: Advances in the biosciences* (Vol. 25, pp. 451-460). Oxford, England: Pergamon Press.
- MEYERSON, B. J., & LINDSTRÖM, L. H. (1973). Sexual motivation in the female rat: A methodological study applied to the investigation of the effect of estradiol benzoate. *Acta Physiologica Scandinavica* (Suppl. 389), 1-80.
- MONEY, J. (1987). Sin, sickness, or status? Homosexual gender identity and psychoneuroendocrinology. *American Psychologist*, **42**, 384-399.
- MONEY, J., & MATTHEWS, D. (1982). Prenatal exposure to virilizing progestins: An adult follow-up study of twelve women. *Archives of Sexual Behavior*, **11**, 73-83.
- MONEY, J., SCHWARTZ, M., & LEWIS, V. G. (1984). Adult erotosexual status and fetal hormonal masculinization and demasculinization: 46,XX congenital virilizing adrenal hyperplasia and 46,XY androgen-insensitivity syndrome compared. *Psychoneuroendocrinology*, **9**, 405-414.
- MOORE, C. L. (1984). Maternal contributions to the development of masculine sexual behavior in laboratory rats. *Developmental Psychobiology*, **17**, 347-356.
- POMERANTZ, S. M., ROY, M. M., THORNTON, J. E., & GOY, R. W. (1985). Expression of adult female patterns of sexual behavior by male, female, and pseudohermaphroditic female rhesus monkeys. *Biology of Reproduction*, **33**, 878-889.
- RICHARD, A. F. (1985). *Primates in Nature*. New York: Freeman.
- ROBATAILLE, J. A., & BOUVET, J. (1976). Field observations on the social behaviour of the Norway rat, *Rattus norvegicus* (Berkenhout). *Biology of Behaviour*, **1**, 289-308.
- SIGNORET, J. P. (1970). Reproductive behaviour of pigs. *Journal of Reproduction & Fertility* (Suppl. 11), 105-117.
- SLOB, A. K., DE KLERK, L. W. L., & BRAND, T. (1987). Homosexual and heterosexual partner preference in ovariectomized female rats: Effects of testosterone, estradiol and mating experience. *Physiology & Behavior*, **41**, 571-576.
- SMUTS, B. B. (1986). Sexual competition and mate choice. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 400-412). Chicago: University of Chicago Press.
- STOCKMAN, E. R., CALLAGHAN, R. S., & BAUM, M. J. (1985). Effects of neonatal castration and testosterone propionate treatment on sexual partner preference in the ferret. *Physiology & Behavior*, **34**, 409-414.
- WINGFIELD, J. C., NEWMAN, A. L., HUNT, G. L., & FARNER, D. S. (1982). Endocrine aspects of female-female pairing in the Western gull (*Larus occidentalis wymani*). *Animal Behaviour*, **30**, 9-22.
- YOUNG, W. C. (1961). The hormones and mating behavior. In W. C. Young (Ed.), *Sex and internal secretions* (Vol. 2, pp. 1173-1239). Baltimore: Williams & Wilkins.
- YOUNG, W. C., GOY, R. W., & PHOENIX, C. H. (1964). Hormones and sexual behavior. *Science*, **143**, 212-218.