The Role of Maternal Stimulation in the Development of Sexual Behavior and Its Neural Basis[a]

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The study of sexual development and sex differences has been one of the most active research areas in developmental psychobiology during the past three decades. Much of this work has been guided by the important discovery that male mammals secrete testosterone during embryonic or neonatal life. This discovery led to an explosion of experiments based on the manipulation of testosterone and related steroids during early developmental stages — experiments that identified hormonal effects on the development of a wide range of behavioral, physiological, and anatomical characters. The success of this approach has often left the impression that hormones act alone to organize the nervous system and that the prenatally or neonatally organized nervous system, in turn, determines the particular form that adult behavior will take.[1] However, the developmental effects of any factor are exerted within a psychobiological context of multiple determinants. For any given level of a particular hormone, these additional factors can alter developmental outcome. Furthermore, these factors can influence the pathway through which an effect of the hormone is exerted.

My own interest has been directed toward investigating the contributions of afferent input from the species-typical maternal environment to both sexual development and the emergence of sex differences in behavior. In this paper, I will describe some of the interrelationships between maternal stimulation and the hormonal condition of her pups and identify some specific contributions of maternal stimulation to behavioral and neuroanatomical development. I will also attempt to articulate some differences between understanding sexual development within an individual and understanding sex differences, which are matters of individual differences. Finally, I will raise the question of whether the maternal effects on masculine sexual development that have been found can be understood in terms of functional consequences for successful reproduction.

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CHARACTERISTICS OF EARLY STIMULATION

A rat is born with sealed eyes and ears, into a nest with many littermates and a single parent. The nest, littermate huddle, and many actions of the dam maintain homeostatic conditions required for survival and growth of this altricial mammal. Until the infant gains the sensory and motor competence to venture forth, its sensory world is constrained by the warm and familiar context of the nest.

Relative stability is a major adaptive consequence of the cohesion of dam, litter, and nest, but it would be a mistake to conclude that the environment of an infant rat lacks stimulation. The huddle stirs in constant slow motion, with pups on the top burrowing to the center as those on the bottom revolve to the top.[2] The dam alternates long bouts of nest attendance with time off to eat, rest, and groom. Each of her reentries to the nest brings chemical, thermal, tactile, and vestibular stimulation to her young. She brushes against and sometimes steps on pups as she shifts position over them; she nuzzles, mouths, licks, and manipulates them, moving them to and fro, and selects some to lick intently. Once settled into the crouching posture in response to the active probing of her thoroughly aroused pups, the dam becomes quiescent and the pups suckle in unison.[3] Even then, however, the steady suckling is punctuated by the periodic letdown of milk. A mouthful of milk elicits swallowing and a vigorous stretch reflex from each pup, who often then releases the nipple and searches for another.[4] Thus, events within the nest and the reactions of the young pups to them provide a rich, reliable stimulus environment that can be used to shape early behavioral development.

The dam is the primary source of stimulus flux for nest-bound infants. Dams differ from one another in patterns of nest attendance and levels of maternal behavior while in the nest, but much of the stimulation each dam provides is given simultaneously to all littermates (e.g., warmth and touch from crouching over them; tastes and odors carried on her body) or is randomly distributed among them (e.g., contacts while shifting position). However, licking and the handling that is associated with it are directed to pups one at a time. In conjunction with individual differences in pup attractiveness, this maternal behavior readily produces different stimulus levels for individuals within the same litter.[5]

VARIATION IN LEVELS OF MATERNAL LICKING

Several studies support the conclusion that two distinct behavioral patterns are subsumed under the label "maternal licking." Maternal licking that is directed to the perineum of pups is controlled by sensory and motivational mechanisms that are different from those controlling body licking, which includes snout and oral contact with the general body surface.[5] Perineal or anogenital licking (AGL) occupies more maternal time, occurring at rela-

tively constant, high levels throughout the first 2 weeks postpartum before declining to relatively low levels by the end of the third week.[6] This coincides with the period during which pups require external stimulation to urinate and defecate. Body licking is more variable, but increases slightly toward the end of the second week, perhaps because grooming of the emerging fur is included in the category.[5] There is no evidence as yet that particular individuals are singled out for a disproportionate share of body licking, but males clearly receive more perineal licking than do their female siblings throughout the period during which this maternal behavior is performed.[6]

The biased stimulation of pups as a result of maternal AGL originates with the perinatal difference in the level of testosterone available to male and female infants.[7] The bias can be reversed by providing testosterone to females on the day of birth (FIGURE 1). Idiosyncratic differences among individual males and females, perhaps accounted for by individual differences in testosterone level, can also elicit systematic differences in level of maternal AGL. For example, male rat pups gestated by dams that were stressed by having been crowded during pregnancy elicit less licking than normally gestated males,[8] and female gerbils exposed to elevated prenatal levels of testosterone as a result of having been gestated next to males elicit more maternal licking than females gestated at a greater distance from males.[9]

Chemical stimuli carried in the urine of pups are important for eliciting
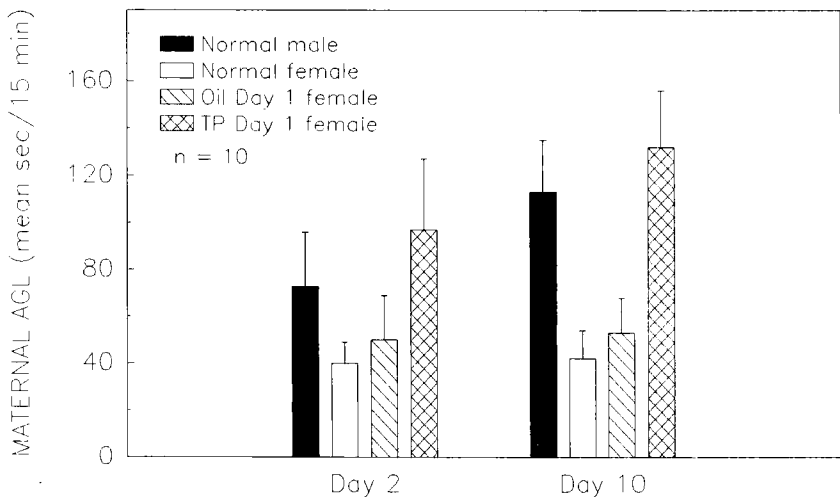

FIGURE 1. Maternal anogenital licking (AGL) during 15-minute presentations of 3 similarly treated foster pups. Treated pups were injected on the day of birth (day 1) with 0.5 mg testosterone propionate (TP) in 0.05 ml cottonseed oil. The differences between males and females and between oil- and TP-treated females were significant on both test days. (Reprinted from Reference 7 with permission. Copyright 1982 by the American Psychological Association.)

maternal licking, for guiding a dam to lick particular pups within the litter, and for directing her licking to the perineal region. Male urine is more effective than female urine for each of these functions. When dams are confronted with the opportunity to investigate two drops of urine, one from a male and the other from a female pup, presented on paper in an arena apart from the nest, they consistently direct more attention to the male urine.[10] When a piece of filter paper bearing a drop of urine from a male pup is placed inside their nests, dams respond by initiating a bout of maternal AGL; female urine is no more effective than saline.[10] When the urine is dropped on the skin of pups, dams direct licking to the treated pup, with particular attention to the region of skin bearing the scent.[11,12] Both male and female urine is effective in this context, but male urine—whether placed on males or females—leads to more licking.[11]

The preputial glands are one source of chemosignals that attract maternal licking.[12-14] These modified skin glands are found in both sexes, and they release their products through ducts that terminate near the urethral opening. Dodecyl propionate is a preputial chemosignal that has been isolated and identified as an effective elicitor of maternal AGL; it is produced by both sexes.[13] However, there is a functional difference in the preputial glands of the two sexes. Preputial gland removal eliminates the sex bias in maternal attention to pup urine, and preputial gland homegenate from male pups elicits more attention than an equal volume of homegenate from females.[14] Whether maternal discrimination is based on qualitative differences in chemosignals produced by the two sexes or on a sex difference in concentration of the same attractive chemical(s) is unknown.

There is some evidence that pups also influence the amount of licking that they receive by behavioral means. Male pups release a larger volume of urine with a longer latency after the onset of perineal stimulation.[15] Both of these factors have the effect of increasing the duration of a bout of licking. Males are also more likely than females to assume the characteristic leg extension response to perineal stimulation.[16] This response, which includes a supine, immobile posture with legs and tail extended, reliably precedes urine release and apparently assists the dam in her licking.

Recycled nutrients from pup urine are significant components of the maternal diet, and the motivation of dams to lick their pups includes an appetite for the salts and water in pup urine.[17] Differences in motivation for these dietary elements result in differences in the frequency, intensity, or duration of licking among dams. Dams may also differ in their ability to detect or in their interest in pup chemosignals. Differences among dams in propensity to lick add to the variation in maternal licking that results from differences among pups as elicitors of licking. Thus, although all developing pups must receive a minimal level of perineal stimulation in order to survive, there are reliable between- and within-litter differences in the amount of this stimulation that each pup receives during the course of early development.

MATERNAL ANOGENITAL LICKING AS
PUP STIMULATION

During anogenital licking, a dam typically uses her forepaws to turn the pup to a supine posture, with its head tucked under her. The light pressure of her body against its throat and chest has a quieting effect that inhibits the righting reflex. The dam holds the pup, usually by encircling its flanks with her warm forepaws. She then begins to lick the perineal skin with rhythmic, lapping movements. Tactile stimulation of the perineum and surrounding skin, but not other body regions; elicits the leg extension response from pups. If the pup responds, licking will continue until urine is released and consumed.[16] Odors on the ventral surface and vaginal area of the dam are readily available to a pup held for licking in the typical posture. In addition to eliciting specific postural adjustments, skeletal reflexes, and eliminative reflexes, AGL changes the arousal level of pups.[18] Thus, a bout of anogenital licking provides a characteristic cluster of vestibular, thermal, tactile, olfactory, kinesthetic, and autonomic changes for pups; these bouts are repeated several times daily throughout early development (FIGURE 2).

In addition to eliciting adaptive responses from pups that meet immediate survival needs, maternal stimulation has more general developmental conse-

FIGURE 2. A maternal rat performing anogenital licking. The close-up shows the characteristic orientation and the infant's leg-extension response.

quences for young rats. Tactile stimulation of the body surface provided by licking, handling, and contact with the dam's moving body affects growth by supporting both the release and the utilization of growth hormone and corticosterone by pups.[19] Such stimulation is also reinforcing for young infants: they will learn to approach odors that have been associated with a dam, or with stimulation that an experimenter provides with a brush so as to mimic maternal licking, handling, and contact.[20] Repeated pairings of tactile stimulation with a particular odor will lead to enduring changes in both behavioral responsiveness and the functional anatomy of the olfactory bulb.[21]

There have been no studies to compare the relative reinforcing properties of tactile stimulation applied to different body regions, and most studies using tactile stimulation as a reinforcer combine perineal with other body stimulation. In a study designed to determine whether tactile stimulation that is restricted to the perineum is a sufficient reinforcer, 18 males, 10–12 days of age, were placed, in pairs, into a warm environment permeated with the scent of wintergreen. Each pup was allowed to crawl into a holder, fashioned from rubber tubing lined with soft sponge, where they remained for 10 minutes. For 10 seconds during each minute, one member of each pair was rotated to a supine position and stroked only on the perineum with a soft brush; the other was exposed to wintergreen odor for the same amount of time, but was not stroked. An additional 9 controls were neither exposed to wintergreen nor stroked. After a 30-minute rest away from wintergreen, the pups were given 10 consecutive trials, at 4-minute intervals, in a Y-maze, with wintergreen scent in one arm but not the other. Each pup was given 40 seconds on each trial to enter fully into an arm of the maze. The groups did not differ in level of responsiveness: a choice was made on about half of the trials in each group. However, the groups made different choices. Pups in each control group chose the scented arm less than half of the time, whereas stroked pups chose the wintergreen arm over 80% of the time (FIGURE 3).

This study demonstrates that tactile stimulation that is restricted to the perineum is a sufficient reinforcer for young infants to develop an attraction to an initially aversive odor. However, many forms of stimulation, even electric shock,[22] can reinforce the formation of an attraction to novel odors in young infant rats. As Johanson and Terry have remarked,[20] it would be interesting to discover whether there is any specificity in the route of reinforcing stimulation and the behavioral or contextual nature of enduring responsiveness among adults to odors experienced during infancy.

Although the complete interaction pattern during maternal licking invokes a complex set of stimuli that engages several of the infant's modalities, the licking itself is focused on the perineum. The pattern of somatosensory input to the spinal cord from receptive fields involved in the control of lordosis has been mapped in studies of adult female rats. Inputs from pressure receptors in the skin of the perineum, posterior rump, and tail base are carried in the sensory branch of the pudendal nerve and enter the spinal cord at the dorsal roots of L5, L6, and S1.[23] Stimulation of these skin regions is
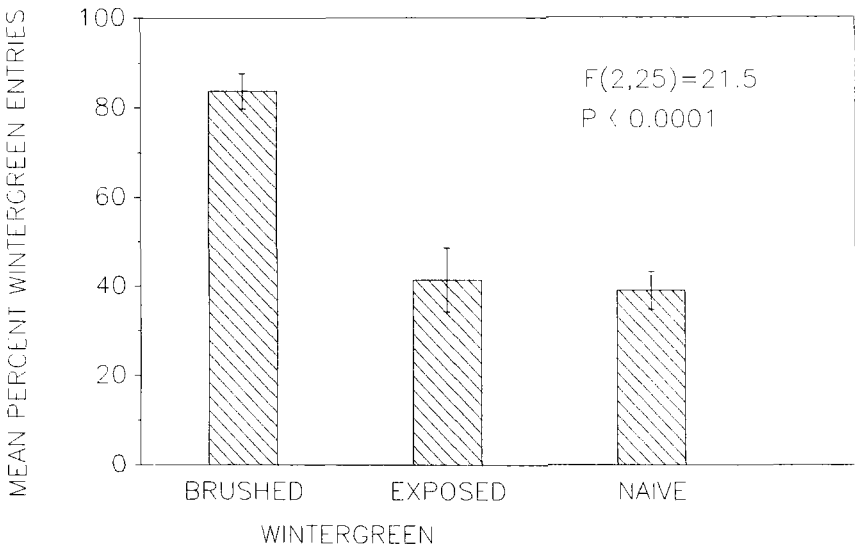
FIGURE 3. Brush stimulation of the perineum (10 seconds/minute for 10 mintues) that is paired with exposure to wintergreen leads to an attraction to that odor in 10- to 12-day-old male pups tested in a Y-maze.

a highly effective elicitor of both adult lordosis[23] and the infantile leg extension response.[16] Both infantile leg extension and adult lordosis to tactile stimulation can be blocked by local anesthesia of these regions. Furthermore, it is in precisely these regions that the major share of maternal anogenital licking is concentrated. Thus, if somatosensory mechanisms are organized similarly in adults and infants, there are significant levels of maternally provided input entering the spinal cord at the lumbar-sacral transition.

In adults, afferent input from the perineum and surrounding areas is carried to preoptic and hypothalamic brain regions where it figures importantly in many neuroendocrine and behavioral mechanisms involved in reproduction.[24] Again, if input follows similar pathways in infants, the regions of the developing nervous system that will later underlie reproduction receive reliably high levels of afferent input from the licking behavior of the dam.

Electrophysiological studies of infant rats reveal that afferent connections to and within the hypothalamus develop primarily during the early postnatal period.[25,26] The time course overlaps with the postnatal production of gonadal steroids and the postnatal contribution of these steroids to the developing nervous system. There is, furthermore, evidence to support the idea that the developmental effects of gonadal steroids on the hypothalamic-preoptic area require concurrent afferent input: pharmacological and surgical procedures that block afferent inputs to the hypothalamic-preoptic area interfere with the

organizational effects of neonatal steroids on neuroendocrine and behavioral function.[27] Therefore, conditions in the developing nervous system are such that maternal stimulation could play an important formative role, particularly in conjunction with the primary actions of gonadal steroids.

MATERNAL STIMULATION, SEXUAL DISSIMILATION, AND SEXUAL DIFFERENTIATION

Behavioral sex differences in rats are not absolute: both males and females are capable of the full rat repertoire. Yet, the two sexes differ in a variety of behavioral patterns. Sex differences in behavior reflect differences in the threshold, rate, sensitivity, intensity, completeness, or other quantitative aspects of the components that constitute the behavior. Sex differences, like other individual differences, arise out of the developmental processes through which each of the behavioral patterns is organized within an individual. For a developmentalist, the term "differentiation" refers to the progressive elaboration of morphologically and functionally distinct systems out of uniform, undifferentiated beginnings within an individual. Thus, for sexual behavior and reproduction, these developmental processes are referred to as sexual differentiation. Of course, "differentiation" is in more general use to refer to the formation of any difference. In that sense, "sexual differentiation" is also used to refer to the formation of differences between individual males and females, whether or not these differences have anything to do with reproduction. These individual differences in behavior may arise from individual differences in sexual differentiation (strict sense), but they need not. Therefore, I suggest that it can be useful to have a more neutral term, "sexual dissimilation," to refer to the formation of individual differences between the sexes, leaving "sexual differentiation" to refer unambiguously to the development of sexual behavior and reproductive systems within an individual.

The degree of dissimilarity of the sexes varies considerably from one behavioral pattern to another: some differences are apparent in one context but not another, whereas others occur across the range of natural contexts. Play is an example of the former, and sexual behavior is an example of the latter.

The degree to which the sexes differ in some behavioral patterns can be modified by the amount of maternal stimulation provided through anogenital licking of developing infants. The normal sex bias in maternal stimulation may, therefore, contribute toward the sexual dissimilation of behavior. If greater stimulation were to make male-typical behavior more likely or more complete, then the typical within-litter variation in stimulation could account directly for some portion of the sex difference in developmental outcome. This seems to be the case for masculine sexual behavior, but not for play. This disparity suggests that not all sex differences, or the maternal contributions to them, rest on a common underlying mechanism.

Pouncing and wresting are forms of active contact play readily observed

among juvenile rats. Both sexes engage in this play but, when sex differences are found, males do more of it.[28] If biased maternal stimulation mediates the sex difference in a straightforward way, males reared by dams who stimulate them less ought to play less. However, the opposite result is found. When maternal AGL was reduced by the use of perfume to mask the dam's reception of chemical stimuli,[29] by peripheral disruption of olfaction in the dam,[5] or by providing the dam with dietary salt so as to reduce her motivation to lick,[5] male offspring performed higher levels of active contact play than normally stimulated controls. Thus, sex differences in play are increased rather than diminished by reduced stimulation.

One possible explanation for these apparently paradoxical results is that general activity level is altered by maternal stimulation, with greater offspring activity associated with lesser maternal AGL. This pattern is consistent with the typical sex difference in activity level, and there is some evidence that open field activity is greater in males reared by dams that provide reduced stimulation.[5] Therefore, the observed maternal effect on play may be indirect, reflecting an interaction between an animal's activity level and some other internal or external factors that dispose males to play more than females. If this reasoning is correct, it might help to explain the inconsistent observation of sex differences in play across different studies.[28]

The contribution of maternal stimulation to sex differences in masculine sexual behavior is apparently more direct than is the contribution to differences in play. Although females can perform masculine sexual behavior, they are less likely to do so and their performance is deficient in a number of ways. Decrements in masculine sexual behavior are observed in both males and females reared by dams that provide reduced perineal stimulation.[30] The converse is also true: enhanced masculine sexual behavior results when females are provided with extra perineal stimulation during infancy.[31] Therefore, the reliable sex bias in maternal stimulation may account for some of the typical dissimilarity between the sexes in the degree to which mechanisms underlying masculine sexual behavior are developed.

The function of masculine sexual behavior is to fertilize eggs. Females, by definition, have no sperm with which to accomplish this; masculine sexual behavior can have no function for them. The argument that it would be maladaptive—risky and wasteful—for them to devote time to this pursuit is persuasive. However, the constraints of developing systems are such that it may be impossible for females to develop into functional adults without also developing at least some masculine copulatory mechanisms—and vice versa for males. A functional dilemma can be avoided by keeping in mind the distinction between the performance of behavior and the development of competence to perform it. In the usual course of events, females do not engage in masculine copulation, nor do males engage in feminine copulation. They lack the motivation to do so, in large part because they do not secrete adequate levels of the appropriate hormones. The degree to which they have the underlying capacity for the behavior may be irrelevant from a functional

point of view. Indeed, much of sexual differentiation is identical for males and females within the same species, although species differ in the extent of sexual dissimilarity that emerges during the differentiation process.[32] It is for this reason that I have chosen to use "sexual dissimilation" to refer to developmental processes that produce sex differences and "sexual differentiation" to refer to the development of sexual capacity.

Although much of development among rats is shared by males and females, the testosterone secreted by males during early development both plays an important role in masculine sexual differentiation and originates a number of well-known sex differences. Testosterone and its metabolites alter developmental outcomes in many developing systems through effects that cascade from direct effects on the migration, survival, growth, and activity of cells.[33] Biased maternal stimulation as a result of differential chemosignal production by neonatal scent glands is an element in the early developmental nexus that can be traced to testosterone. It contributes both to some sex differences and to masculine sexual differentiation. In order to determine whether either or both of these effects are functionally significant, it is necessary to examine the details of the maternal effects.

MATERNAL STIMULATION AND MASCULINE REPRODUCTION

The sexually biased maternal anogenital licking stems from the differential production of chemosignals by males and females. Therefore, it has been possible to study the developmental effects of this form of maternal stimulation by interfering with the dam's ability to detect chemical stimuli from her pups. In one study, polyethylene tubing was used to line the nasal passages of dams from the day of parturition until two weeks later.[30] This procedure prevents odors from reaching the olfactory epithelium,[34] and was effective in reducing both forms of maternal licking in treated dams. The offspring were gonadectomized as adults, given identical testosterone replacement, and tested for masculine sexual behavior with hormone-primed female partners. Males reared by the treated dams had longer latencies to ejaculate and to resume sexual behavior after ejaculating; they also had longer intervals between intromissions. Regardless of rearing condition, females did not perform the motor pattern that is characteristically associated with ejaculation in males. However, the behavior of their dams did affect their performance of masculine sexual behavior: females reared by the treated dams were less likely to mount or to perform the dismount that characterizes intromission in males.

In a second, converse study, females were stroked daily with a small brush to provide them with extra perineal stimulation as neonates and then treated with testosterone as adults.[31] These females were more likely to mount a female partner and more likely to perform the intromission dismount

pattern than were shoulder-stimulated sibling controls. These results, in com-
bination with the nasal intubation study, allow one to conclude that some of
the sex difference in ability for masculine sexual behavior can be accounted
for by the differential stimulation males and females receive as neonates.
However, regardless of level of infantile stimulation, the adult performance
of the behavior requires conditions, such as adequate levels of testosterone,
that are common for males and rare for females. It seems unlikely, therefore,
that the sex bias in maternal anogenital licking has evolved to make the sexes
different from one another. The differences that do emerge during develop-
ment may simply be a byproduct of selection for other functional conse-
quences. One possibility is selection to improve the development of copu-
latory mechanisms in sons so that they will be better able to compete with
other males.

The nasal intubation procedure reduced maternal anogenital licking, but
it also reduced body licking and produced distress in some of the treated
dams.[30] Therefore, the method for altering anogenital licking has recently
been refined.[5] A method that works well to reduce anogenital licking while
having little if any effects on other components of maternal behavior is re-
peated (days 1, 2, 3, 5, 8, 11, 14 postpartum) peripheral treatment with very
small quantities (0.05 ml) of 5% zinc sulfate solution while the dam is anes-
thetized briefly with ether. Application as a nasal spray permits small doses
and apparently avoids systemic side effects that can accompany irrigation
methods.[35] We did not observe illness in our dams, and the weight gain of
pups, measured both at the end of treatment and at weaning, could not be
distinguished from controls. We observed no effects on body licking and, if
anything, the treated dams spent slightly more time in the nest, nursing their
pups. However, there was a consistent reduction in anogenital licking
throughout the period during which this behavior normally occurs. FIGURE 4
presents the data from a sample of treated and control dams that were video-
taped for 4 hours daily in the study designed to develop this procedure.

We used the zinc sulfate procedure to rear males with reduced infantile
stimulation. As adults, these males were compared with controls whose dams
had simply been anesthetized on the same schedule as the dams that were
anesthetized briefly during the applications of the zinc sulfate nasal spray.
Unlike the intubation study, all males were left intact and received no testos-
terone treatment as adults. They were observed with estrous females until
ejaculation had occurred on two separate occasions. Again, a number of quan-
titative differences in the sexual behavior of the males in the two groups was
found. Perhaps the most striking difference was a reduction in copulatory
efficiency for the males reared by the less stimulating dams (FIGURE 5). Cop-
ulatory efficiency refers to the proportion of mounts that include an intro-
mission, as inferred from the characteristic form of the dismount.

We have also recently examined the effect of maternal stimulation on the
copulatory behavior of males that mated to sexual exhaustion—i.e., until
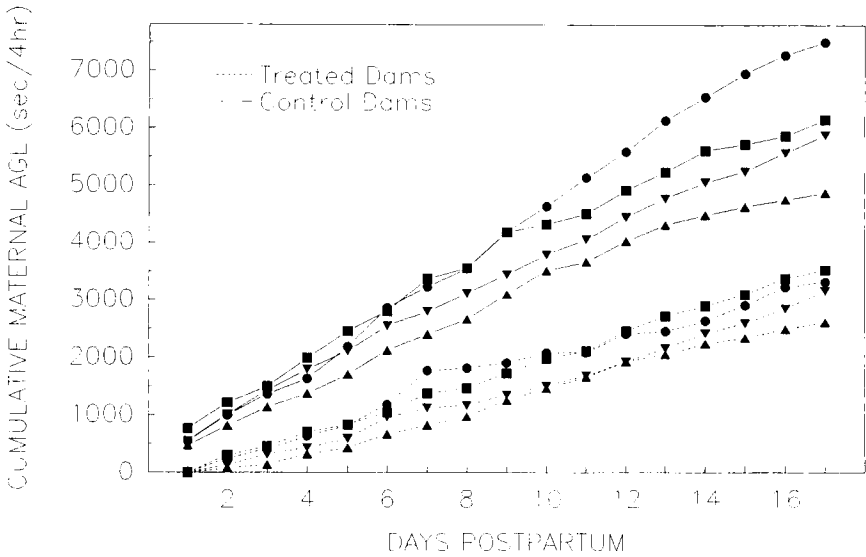the male ceased copulating for the day—in each of two separate sessions. The

FIGURE 4. Dams with olfactory deficits perform less maternal anogenital licking (AGL) throughout the early development of their pups. Deficits were imposed by repeated treatment with zinc sulfate applied in small doses as an intranasal spray. Measurements were made from videorecordings of dams and their litters of 8 pups (half male, half female), taped in red light in time-lapse mode for 4 hours each day in the early part of the dark phase of the light cycle. Each curve represents a single dam; the 2 dams sharing a symbol were observed at the same time.
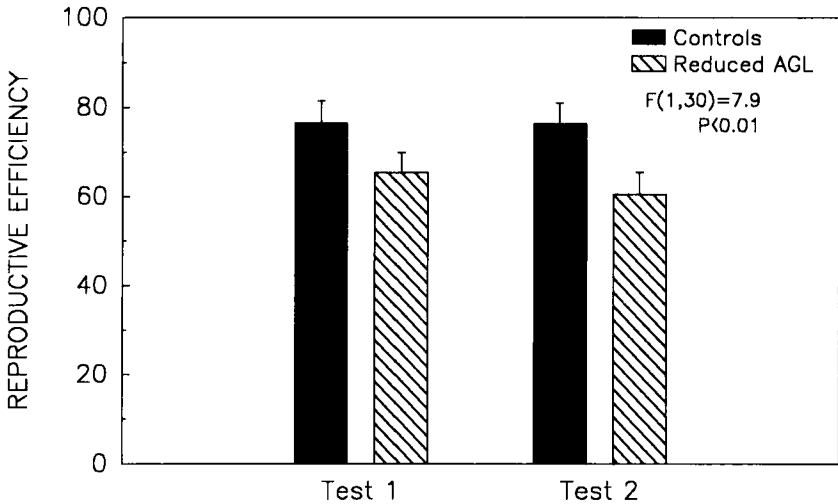

FIGURE 5. Male offspring of dams that provided them with low levels of anogenital licking as a result of zinc sulfate treatment were less likely to perform an intromission pattern upon mounting a female (reproductive efficiency) than were normally stimulated control males. The data are from 2 separate tests, each with one ejaculation.

reduced reproductive efficiency among sons of dams that provided reduced stimulation was found to persist throughout the two separate exhaustion series, each of which included multiple ejaculations over approximately 2 hours.[36]

Similar effects of maternal stimulation on masculine sexual behavior have been found by others, using perfume to mask the dam's reception of chemosignals.[29] Although the maternal effect has been relatively small in magnitude in each study, it does seem to be reliable across different methods of manipulating the dam and may play a biologically significant role in the normal development of males.

It is possible that enhanced maternal licking of males has evolved specifically for its contribution to increasing the probability of leaving second-generation offspring through sons. Clearly, males can grow and develop all of the components of masculine copulation with female-typical levels of stimulation. Although there is currently no direct evidence that the behavioral consequences of maternal stimulation would serve to enhance reproductive competition of sons, the quantitative changes in copulatory behavior that have been found after manipulation of the stimulation are suggestive of such an effect.

Rats have a polygynous mating system with male competition. Sperm competition during multiple ejaculations with the same female accounts for a great deal of the differential reproduction among males.[37] Reliable and appropriately timed intromissions and ejaculations are obvious behavioral components of this competition. Although it is unlikely that the relatively small maternal effects on masculine copulation that have been observed, such as those on ejaculatory latency and the probability of performing an intromission with each mount, would affect the male's ability to impregnate a female encountered in isolation, it is entirely possible that such effects would alter the outcome of sperm competition.

MATERNAL STIMULATION AND NEURAL DEVELOPMENT

Sperm competition is also affected by the penile reflexes that accompany copulatory behavior.[38-40] Penile reflexes are used during ejaculation to place a sperm plug so that it adheres to the female's cervix, which is a necessary condition for transcervical transport. During nonejaculatory intromissions, the reflexes dislodge the sperm plugs placed by competitors and disrupt transcervical transport. These reflexes are controlled by striated penile muscles and their motor neurons, which are located in sexually dimorphic nuclei of the lumbar spinal cord.[41]

One such nucleus is a dorsomedial nucleus in L5-L6 that innervates the bulbospongiosus muscles which encircle the bulb of the penis.[42-44] (These muscles have also been called bulbocavernosus muscles, and the nucleus has been named the spinal nucleus of the bulbocavernosus, SNB.)[42] Contraction

of the bulbospongiosus muscles leads to complete erections with a flared tip to the penis and plays a role in ejaculation, formation, and placing of copulatory plugs; it is also used during removal of plugs placed by other males.[38-40] It is possible that maternal stimulation could affect the outcome of sperm competition by altering the development of this neuromuscular system.

We reared animals with dams that were treated with zinc sulfate, as described previously, or with control dams.[45] The treated dams provided reliably lower levels of maternal anogenital licking, but no detected differences in other aspects of maternal care. When the male and female offspring were adult, motor neurons in each section throughout the extent of the SNB were counted. We found that reduced perineal stimulation during infancy led to significantly fewer neurons in both males and females, but no change in neuron size. The maternal effect, which resulted in an 11% reduction in motor neuron number, was restricted to a rostral population of neurons within the SNB. There was no effect on gross lumbar spinal cord dimensions or body weight. Therefore, there was apparently no generalized effect on neural development or body growth.

It will be recalled that afferent input from perineal stimulation enters the spinal cord at the lumbar-sacral transition,[23] in the same segments in which the effect on adult motor neuron number was observed. It is possible, therefore, that the effect was mediated by a change in the level of local trophic factors, produced either by the afferents to the motor neurons or by the target muscles. Target effects on motor neuron survival are well known.[46] The sexual dimorphism in the SNB[47] stems largely from the fact that penile muscles atrophy in female neonates but are maintained in males because of masculine levels of testosterone.[48] Fewer neurons die in males than in females because of the sex difference in target.[41] However, a sex difference in afferents might also have this effect: dorsal root ablation in chick embryos leads to increased death of lumbar motor neurons, an afferent effect that is independent of the role of target muscles.[49]

It is also possible that the maternal effect on motor neuron number was mediated by some more systemic factor, such as the secretion of a hormone. The specificity of the effect argues against a hormone having generalized effects, such as growth hormone, but it is possible that differential testosterone secretion could explain the effect. If maternal stimulation of the perineum promotes testosterone secretion, then the effect could be accounted for by the well-established effect of this hormone on target muscle. Of course, this mechanism would explain the effect in developing females only if there were also a route by which maternal stimulation could increase endogenous levels of testosterone in this sex. At this point, there is no evidence with which to choose among the several plausible mediators of maternal stimulation on adult neuron number.

These results are exciting because they are the first demonstration that predictable, species-typical, afferent input from a natural source can affect

the adult morphology of a sexually dimorphic nucleus in the central nervous system. They demonstrate that stimulation provided by a dam during the normal course of caring for developing young can contribute to the differentiation of neural mechanisms that underlie masculine sexual behavior. Variation among the dams that provide this stimulation can produce individual differences in neural mechanisms among males that may, in turn, affect their reproductive success. Finally, the results lead one to conclude that reliable differences in the stimulation provided to males and females contribute toward the sexual dissimilarity of nervous system morphology.

SUMMARY AND CONCLUSIONS

Both sexual differentiation, which is a matter of individual development, and sexual dissimilation, which is a matter of individual differences, result from developmental processes that are open to input from the early maternal environment. There are reliable features in both the dam and the young that ensure that males receive more perineal stimulation from maternal licking than is necessary for survival and normal growth. This stimulation contributes toward the development of masculine sexual behavior and mechanisms in the central nervous system that control copulatory reflexes. Because of differences in signals that they produce, males receive more stimulation than females. This bias in early stimulation accounts for some of the dissimilarity between the sexes in nervous system morphology and behavior. The same processes that produce sex differences can also produce individual differences among males. These differences are likely to have significant functional consequences in rats, a species in which males have a high level of intrasexual reproductive competition. Future research will be directed toward testing this functional hypothesis and toward exploring the extent of stimulative effects on the development of the sexually dimorphic brain regions that function in sexual behavior.

ACKNOWLEDGMENTS

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