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suggestion that at least some aspects of early postnatal motor behaviors, such as walking, can develop normally in chicks even when embryonic motility is abnormal. However, detailed studies using quantitative analysis of electromyograms (EMGs) and kinematic data are needed to answer this question definitively. Recent studies by William Smotherman and Scott Robinson suggest that sensory stimulation before birth in rat fetuses can alter behavior after birth.

See also Behavioral Plasticity
Development—*Intrauterine Position Effect*
Neuroethology

Further Resources

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Anne Bekoff

Development
Intrauterine Position Effect

If you were to look inside a pregnant gerbil, rat, mouse, or most other small rodent you would find her fetuses lined up like peas in a pod, with male and female fetuses randomly distributed within each of the two horns of her uterus. Consequently, you could describe each fetus in terms of its own sex and that of its immediate intrauterine neighbors. A male fetus situated between two male sibs could be described as a two-male fetus (2M male); a female residing between two female fetuses as a two-female fetus (2F female), and so on.

Results of many studies conducted during the last 25 years have shown that the position that a fetus occupies in the uterus, relative to its male and female siblings (its *intrauterine position* or IUP), has life-long effects on its physiology, morphology and behavior. These "intrauterine position effects" are the subject of this article.

To study IUP effects in animals giving birth to more than two young at a time, infants have to be delivered by Caesarian section to determine where they were in relation to one another in the uterus. They then have to be marked permanently so that fetuses from different IUPs can continue to be identified as they mature, and they have to be given to foster parents to rear, because following surgery, mothers may fail to take proper care of their young.

IUP effects exist because male fetuses have higher levels of testosterone in their blood than do female fetuses, and female fetuses have higher levels of estradiol in their blood than do their brothers. These gonadal hormones diffuse from each fetus to its intrauterine neighbors. Consequently, 2M fetuses of both sexes have higher levels of testosterone than do 2F fetuses of the same sex, and 2F fetuses of both sexes have higher circulating levels of estradiol than do 2M fetuses of the same sex. As you might expect, fetuses located adjacent to only one male and/or one female fetus have intermediate levels of estradiol and testosterone, and in adulthood are intermediate between 2M and 2F animals of the same sex in many characteristics.

One important result of studies of IUP effects has been to demonstrate the amazing susceptibility of fetuses during sensitive periods in development to very small differences in exposure to hormones. For instance, the difference in serum testosterone in 2M and 2F male gerbil fetuses is roughly 1.2 nanograms (billionth of a gram) in each milliliter of serum, yet this tiny amount is enough to start a cascade of developmental events that end in profound consequences for reproduction throughout life.

Effects of IUP on males and females of different species are not the same. However, differences between species in effects of IUP should not detract attention from the fact that IUP alters the reproductive life of every species examined to date.

Mongolian Gerbils

Females

The age at which female Mongolian gerbils mature is quite variable. Some show the first signs of puberty before they are 16 days old and while still nursing, others only when 28 days of age or older and already able to live independently. Most unusual, during the period when female gerbils are 22–27 days of age, they very rarely show the first signs of reaching puberty. This strange distribution of rates of maturation is in part an IUP effect. Daughters from 2F IUPs are almost certain to mature early, whereas daughters from 2M IUPs are predominantly late maturing, and age at sexual maturation predicts differences in the lifetime reproductive profiles of female gerbils.

As might be expected, early-maturing gerbil females first reproduce at an earlier age than their late-maturing sisters. Less obviously, early-maturing female gerbils produce more litters during their lifetimes and somewhat larger litters than do late-maturing females, so that early-maturing females produce more than twice as many young during their lifetimes as do late-maturing females. Further, and unexpectedly in view of the strong genetic control of sex of offspring in mammals and the strong effect of IUP on rate of development of female gerbils, litters of early-maturing female gerbils contain more daughters than sons, whereas litters of late-maturing females contain more sons than daughters.

Because there are a greater proportion of female fetuses in the uteri of early-maturing than of late-maturing females, daughters of early-maturing females are more likely to be gestated in 2F IUPs than are daughters of late-maturing females. Thus, mothers and daughters are likely to show similarities in their reproductive life histories because of similarities in their IUPs and, consequently, in their prenatal exposure to gonadal hormones.

Early- and late-maturing female gerbils differ in many aspects of their reproductive behavior. For example, late-maturing females are both better mothers and more aggressive toward unfamiliar males than are early-maturing females. Females that matured early spend less time nursing their young and are less likely to retrieve young that stray from the nest. Late-maturing females are less likely to become pregnant and more likely to attack and injure a male in the weeks following their first encounter with him.

Males

Effects of IUP on male Mongolian gerbils are, if anything, even more profound than the effects of IUP on female gerbils. Fetal male gerbils from 2M IUPs have higher circulating levels of testosterone than do males from 2F IUPs, and this difference in testosterone levels is maintained throughout life.

Perhaps as a consequence of their low testosterone *titers* (concentrations), males from 2F IUPs paired with sexually receptive females are five times more likely to fail to impregnate their partners than are males from 2M IUPs. In fact, a small percent of adult 2F male gerbils have circulating levels of testosterone no different from those of females of their species, and such males never impregnate any females. Perhaps not surprisingly, female gerbils when in breeding condition, but not at other times, prefer 2M males to 2F males.

While 2M male gerbils are more likely to impregnate their mates than are 2F male gerbils, 2F males are considerably better fathers than are 2M males. 2F males generally spend significantly more time in contact with their young, huddled over them and licking them, than do 2M males, and those 2F males that are incapable of impregnating females spend 30 to 50% more time than sexually active 2F males caring for their offspring.

The extra parental effort exerted by 2F males appears to ease the burden on their mates of rearing a litter of young. The average size of second litters reared by females living with 2F males while rearing their first litters is larger than that of females living with 2M males during the same period.

As noted above, males from 2M and 2F IUPs differ throughout life in their circulating levels of testosterone, and differences in parental and sexual activities of male gerbils from different IUPs probably reflect these differences in their testosterone levels. Direct manipulation of the hormone levels of adult male gerbils changes both their sexual and parental behaviors. Males with no testosterone never mate and take very good care of their young, whereas males with artificially elevated testosterone levels are sexually active, but relatively indifferent to their offspring. Thus, testosterone levels in male gerbils, reflecting their IUPs, appear to mediate a trade off between the effort put into directly reproducing and caring for young.

IUP has effects on many behavioral and morphological characteristics of gerbils other than sex and parental behavior. Indeed, everything from whether a gerbil is likely to be right- or left-handed, to the relative size of some structures in its brain and reproductive organs, to its attractiveness to its own parents, is known to be influenced by its IUP. Quite probably, the number of characteristics modified by IUP is greater than we yet know because of the difficulty and expense of studying effects of IUP whether in gerbils or any of the other animals that we consider next.

Mice and Pigs

Intrauterine position has effects on many of the same morphological and behavioral characteristics of other mammals as it does on gerbils, but the direction of IUP effects are sometimes the same and sometimes different. For example, although 2M male mice like 2M male gerbils are more likely to impregnate their partners, and the parental behavior of male mice from different IUPs differ, 2M male mice seem to be more parental and less sexually active than their 2F brethren. In swine, both males and females born in predominately male litters (and therefore more likely to be 2M males) are less likely to conceive as adults than are pigs from litters with relatively few males. Further the relative importance of estrogen and testosterone in mediating IUP effects can differ between species. For example, effects of IUP in gerbils seem to be almost entirely dependent om the testosterone coming from adjacent males, whereas the development of fetal house mice seems to be influenced by the estrogen released by fetal females as well.

Differences in the specific effects of IUP on adult behavior are not unexpected. Although testosterone and estrogen are known to influence the course of development in all vertebrates, their specific effects vary from one species to another. And because IUP effects are a result of differences in prenatal exposure to these gonadal hormones, differences among species in response to hormones should be reflected in differences in the effects of IUP on their development.

Effects of IUP Outside the Laboratory

All of the findings discussed thus far are results of studies carried out in domesticated animals in laboratory settings. Similar effects are known from the wild animals observed in quite natural environments. A particularly ingenious study, in which wild house mice served as subjects, used the oval islands of grass created by the off and on ramps of cloverleaf highway interchanges as enclosures in which to study behaviors of animals from different IUPs under more natural conditions than exist in the laboratory. Wild mice were caught and bred in the laboratory, and their young delivered by Caesarian section, and reared by foster mothers. Once those young had grown to maturity they were released onto highway islands that had been trapped clean of any indigenous inhabitants. The curving highway ramps acted as barriers so that each interchange was a giant cage containing a separate mouse population. Consistent with findings in captivity using female laboratory mice from different IUPs as subjects, 2M females had larger territories than their 2F sisters.

Are There Similar Effects in Humans?

There are surprisingly few studies of effects of sex of uterine neighbors in our own species. Studies that have compared twins of the same and opposite sex have found that women who shared their mother's womb with a brother have more characteristics that some researchers have labeled "male-like" than did twin sisters. However, such an interpretation must be accepted with some caution because "male-like" was often defined in a possibly questionable way, including criteria such as likelihood of using mind-altering drugs and seeking adventure, and susceptibility to boredom. A possibly more convincing, though surely less sensational, study found that sounds produced in the human inner ear, *otoacoustic emissions*, that are more numerous in women than in men, are also more numerous in female members of same-sex twins than in female members of mixed-sex twins. The idea here is that prenatal exposure of female fetuses in mixed-sex twins to testostereone produced by their brothers results in some masculanization of the inner ears of the females, just as in nonhuman animals gestation in IUPs adjacent to males results in masculanization of some body parts of females.

Clearly, much remains to be learned about the role in behavioral development of members of our own species of naturally occurring variation in prenatal exposure to gonadal hormones. IUP effects in nonhuman animals provide important clues as to what sorts of differences in the behavior of male and female humans that experienced different levels of prenatal exposure to gonadal hormones might be looked for.

See also Behavioral Plasticity

Further Resources

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Development
Spotted Hyena Development

Spotted hyenas (*Crocuta crocuta*) are cooperative hunters that, unlike other social carnivorans, live in large groups or *clans* that have an unusually complex social organization. Group members team together to bring down large prey and defend their kills against theft, but surprisingly, they also compete fiercely with each other over access to the spoils. Competition is reflected in rank-related priority of access to the carcass, in favor of females, but is primarily manifested in the speed of consumption: Spotted hyenas appear to show the most extreme case of "scramble competition" of any mammal. Thus, the costs and benefits of group living appear in unusually exaggerated form in this species. Moreover, the female spotted hyena displays the most extreme example of masculinization of any female mammal: Her external genitalia are virtually indistinguishable from those of the male, and she is larger and more aggressive than, and unequivocally socially dominant over, the male. Thus, the traditional mammalian pattern of *sexual dimorphism* (i.e., the differences in form between the sexes) is either absent

Spotted hyena mother and cub, Masai Mara, Kenya.
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