Social Relationships and Social Cognition in Nonhuman Primates

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Complex social relationships among nonhuman primates appear to contribute to individual reproductive success. Experiments with and behavioral observations of natural populations suggest that sophisticated cognitive mechanisms may underlie primate social relationships. Similar capacities are usually less apparent in the nonsocial realm, supporting the view that at least some aspects of primate intelligence evolved to solve the challenges of interacting with conspecifics.

MORE LONG-TERM RESEARCH ON KNOWN INDIVIDUALS has been carried out on wild nonhuman primates than on any other group of animals. Studies have revealed complexities in the social relationships of primates that may be unmatched by other animals. In this article we review some of this research by focusing on three related issues: the functional significance of social relationships, the mechanisms primates use to develop and maintain social relationships, and the cognitive processes that may underlie social interactions. It is not possible in a brief overview to convey the extraordinary diversity of primate societies, and we have been selective in the examples we use, focusing on those species and results that have been most well documented (*1*).

The Functional Significance of Long-Term Bonds

During the last 20 years evolutionary biologists have specified a number of conditions under which particular patterns of social behavior will evolve through natural selection (*2*). A behavior must either increase the reproductive success of the actor (personal fitness) or, if costly to the actor, increase the reproductive success of close relatives enough to offset the cost to the actor's personal fitness (inclusive fitness) (*3*). In animals with long lifespans like primates, it is particularly difficult to demonstrate directly the effects of behavior on fitness. Instead, primatologists often must search for effects that are likely to be correlated with fitness, such as increased access to mates (for males) or decreased interbirth intervals (for females).

Although many studies of insects, birds, and mammals have documented the functional significance of single interactions such as fights, the reproductive benefits of long-term social bonds are less immediately obvious. Three examples drawn from nonhuman primates illustrate the possible function of such bonds.

Female Kinship Bonds

Long-term bonds among related females have been best documented in the semiterrestrial Old World monkeys that live in multimale, multifemale groups: savannah baboons (*Papio cynocephalus*), macaques (*Macaca* spp.), and vervet monkeys (*Cercopithecus aethiops*). In these species, females remain throughout their lives in the groups in which they were born, whereas males migrate to other groups around the age of sexual maturation. Male transfer may occur only once or many times throughout a male's life (*4*).

Within each group, adult females can be arranged in a linear dominance hierarchy, usually defined in terms of the outcome of approach-retreat interactions. Two aspects of female dominance relationships are particularly noteworthy. First, females compete to achieve the highest rank possible (*5*). Second, females consistently support their female relatives during agonistic encounters with members of other genealogies (*6, 7*). As a result of these two processes, an adolescent female typically achieves a rank just below that of her mother (*7, 8*).

The cultural inheritance of rank results in stable and predictable dominance relationships among females. However, lower ranking females occasionally successfully challenge their superiors, often with the help of their female kin; when this occurs, entire genealogies may rise in rank as a unit (*9*). Two types of observations illustrate the importance of supportive relationships among female relatives. First, very young animals, even infants, can dominate older and much larger opponents when their female kin are nearby (*10*). Second, high-ranking females usually retain their positions even when their individual fighting ability is compromised by age or injury (*7*).

Long-term supportive relationships with close female kin clearly help female baboons, macaques, and vervets to acquire and maintain dominance rank. But does high rank increase female fitness? Analysis of the relationship between female rank and reproductive parameters such as age at first birth, interbirth interval, and infant survival in many primate groups indicates that high rank often, but by no means always, increases female reproductive success (*11*). It is not understood why female rank correlates with reproductive success in some groups but not in others. Similarly, it is not yet clear why close bonds among related adult females are so pronounced in some species and manifested weakly if at all in apes and many New World monkeys.

Male-Male Alliances

Although male savannah baboons (*Papio cynocephalus*) migrate from their natal groups and seldom associate with close male kin as adults, they nevertheless form alliances with each other during aggressive interactions (*12–14*). Like female baboons, males form

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dominance hierarchies, but their dominance relationships are much less stable than those of females because male rank depends mainly on individual attributes such as fighting ability, which change through time (*15*). Young adult males in their physical prime achieve the highest ranks. These individuals, who tend to be recent immigrants, use their sharp canines and superior fighting ability to win one-on-one encounters with older, less able opponents. However, in some baboon groups, older males develop stable alliances with one another that allow them to overpower younger, higher ranking rivals (*12–14*). These alliances appear to be based on reciprocity, since (i) males tend repeatedly to solicit aid from the same partners, and (ii) males alternate roles of helper and receiver of help (*13, 14*). Males use these alliances mainly to compete for access to sexually receptive females. This tactic allows some males to achieve higher mating activity than expected from their dominance ranks alone (*12–14*).

Alliances among male chimpanzees (*Pan troglodytes*) differ in several ways from those among male baboons; some examples will illustrate these differences. First, in contrast to most Old World monkeys, chimpanzee females emigrate, but males remain in the natal group or "community" (*16*). Thus chimpanzee alliances often involve close kin, such as maternal brothers (*17*). Second, rather than using alliances to compete directly for access to females, male chimpanzees use them to compete for dominance rank and especially the position of top-ranking (or "alpha") male (*17–19*). For the male who acquires alpha rank, the benefits of alliances are clear, since he achieves a disproportionate share of matings (*18–20*). His helper appears to benefit as well, both because the two males may be close genetic relatives and because the alpha male often tolerates copulations by his ally, presumably because he needs the ally in order to maintain his position (*18, 19*). Third, chimpanzee males form groupwide alliances to patrol the boundaries of their communal home range and conduct gang attacks on individuals from neighboring communities (*21*). Groups of males who compete successfully against males from other groups expand their home range and increase the number of females who join their group (*21, 22*). Thus, in both savannah baboons and chimpanzees, coalitionary relationships between males apparently increase male mating opportunities and, presumably, reproductive success.

Male-Female Friendships in Baboons

Long-term bonds between adult female and male savannah baboons provide a third example of social relationships that appear to increase fitness. For example, observations of one baboon troop (EC) (*14*) revealed that the 34 adult females, when not in estrus, interacted infrequently with most of the 18 adult males. However, each female had one or two special male "friends." Friends spent much time together, groomed often, and appeared relaxed in one another's company. Most friendships continued for many months, persisting through periods when the female was either pregnant or lactating and not sexually receptive. Some lasted for at least 6 years. Similar long-term male-female relationships have been observed in other baboon populations (*23*).

Friendships with males appear to provide two types of benefits to females: protection and infant care. Adult males sometimes protect females or juveniles from aggression by other baboons. In the EC troop, 92% of these interventions (n = 70) involved a friend of the victim or of the victim's mother. Observations from several troops show that male friends also develop close bonds with the female's infant (*14, 23–24*). These bonds, which sometimes persist for many years, appear to benefit infants and juveniles in several ways: protection from other baboons (including, perhaps, infanticidal males), protection from predators, increased opportunities to feed on preferred foods, and, in the case of the mother's death, a substitute guardian that may save the infant's life (*14, 23–24*).

What reproductive benefits do males receive from friendship? To answer this question definitively, information about paternity is needed. This is difficult to obtain because female baboons typically mate with several different males during a given estrous cycle. However, during the 2- or 3-day period when conception is most likely to occur, females usually mate with only one or two males, the "likely fathers." In EC troop, about half of the friendships involved such individuals, and in these cases, the main benefit of friendship to the male may have been increased opportunities to contribute to the survival of his own offspring. However, half of the friendships involved males who had never been observed mating with the female. These males may have enjoyed delayed reproductive benefits, since prior friendship was associated with a significantly greater frequency of mating months later when the female was ready to conceive again (*14*).

Developing, Maintaining, and Exploiting Social Relationships

These examples indicate that nonhuman primates cultivate relationships with particular members of their groups and that such relationships contribute to individual reproductive success. Similarly, communicative abilities and social skills that facilitate the development and exploitation of relationships appear to have been favored by natural selection. For example, when juvenile rhesus macaques are threatened or attacked by another monkey, they use vocalizations to solicit assistance from individuals who are out of sight, to communicate the seriousness of the need for help, and to indicate certain characteristics of the opponent (*25*). Spectrographic analysis of tape-recorded screams revealed that juveniles gave acoustically different screams depending on both the intensity of the interaction and the dominance rank and kinship of their opponent. When tape-recorded screams were played back to the juveniles' mothers, mothers responded most strongly to screams that had originally been given during physical contact with higher ranking opponents, less strongly to screams that had been given to lower-ranking opponents, and least strongly to screams that had originally been given to relatives.

Similar methods have been used to investigate mechanisms mediating social reciprocity in vervet monkeys (*26*). The theory of reciprocal altruism predicts that cooperation among nonrelatives can evolve when individuals encounter each other regularly, recognize each other individually, and are capable of adjusting their behavior according to past experience (*27*). The social relationships of male baboon alliance partners and those of male and female baboon friends appear to be based on reciprocal altruism, but in neither case have observers demonstrated a causal relationship between the actions of one partner and the subsequent behavior of the other. Evidence for such a causal relationship was obtained through experiments with wild vervet monkeys (*26*). Observers waited until roughly 1 hour after vervet A had groomed B and then used a hidden speaker to play B a vocalization originally given by A when soliciting support in an alliance. B's response to this solicitation was compared with the response to the same call after a 2-hour period when no grooming had occurred. Results indicated that prior grooming significantly increased B's willingness to attend to A's solicitation for support if A and B were not close matrilineal kin; if A and B were relatives, the magnitude of B's response was unaffected by recent grooming (*26*). These results indicate that monkeys can dispense social benefits (for example, grooming) in exchange for later benefits provided in a different social "currency" (for example, agonistic support). Long-term, reciprocal exchanges may form the basis of many nonhuman primate social relationships, particularly those that do not involve close relatives.

Nonhuman primates invest time and energy forming cooperative relationships with other members of their group (*28*). If conflict severs relationships, then individuals must either forgo the benefits that relationships provide or incur the additional costs of cultivating new ones. Presumably to avoid these costs, nonhuman primates have developed mechanisms for resolving tensions between individuals. For example, among captive chimpanzees and rhesus macaques, friendly behaviors such as grooming (in rhesus) or kissing (in chimpanzees) occur significantly more often within the first half-hour or so after two individuals have fought than at other times, suggesting that these gestures may serve to reestablish bonds disrupted by conflict (*29, 30*).

Social Cognition

As information on primate social behavior continues to accumulate, the complex and multifaceted social relationships of nonhuman primates become increasingly apparent. As in humans, interactions of one type can affect interactions of another, and single interactions often have not only immediate but also long-term consequences for the individuals involved. Nonhuman primates develop distinct relationships with one another that reflect individual characteristics such as age, sex, kinship, rank, and history of prior interactions. They employ a variety of mechanisms for sustaining relationships that combine competitive and affiliative elements, and they seem to be able to adjust their behavior to particular individuals and circumstances. These features of primate behavior raise intriguing questions about the cognitive capacities that underlie social interactions. Certainly nonhuman primates possess excellent memories and advanced learning abilities, but are they also capable of some of the higher cognitive processes that are central to human social interactions (*31*)?

Most research on primate cognition has been restricted to the laboratory. Some of the most intriguing results have emerged from studies of captive chimpanzees. These studies have demonstrated that chimpanzees can learn to use a large variety of relatively arbitrary signs to represent objects (*32*) and that they can be trained to solve problems of transitivity, use analogical reasoning, and develop deliberate deception of others (*33*). Few comparable experiments have been conducted on monkeys, and we do not yet know the extent to which the cognitive abilities of apes and monkeys differ. Moreover, although laboratory experiments employ rigorous controls, they rarely address questions of evolutionary function, and their relevance to the animals' natural social behavior remains unclear. In contrast, when field primatologists have considered the evolutionary significance of intelligence (*34, 35*), they have usually relied on anecdotal accounts rather than systematic observations or experiments. Clearly we need to develop new methods for investigating social cognition that combine the laboratory scientist's rigor with the field worker's emphasis on naturalistic problem-solving and evolutionary function. Below, we describe recent observations and experiments on natural social groups that indicate the direction such research might take. Rather than review all aspects of social cognition, we focus on three issues: the perception of social relationships by the animals themselves, goals and attribution, and social versus nonsocial knowledge. The research that we review suggests that among nonhuman primates, sophisticated cognitive abilities are most evident during social interactions with conspecifics.

Primates' Perception of Their Social Structure

Do the animals themselves recognize the regularities that we observe in their social behavior—regularities associated with factors such as age, kinship, dominance rank, and previous interactions? We can begin to consider this question by looking at relationships among matrilineal kin in many Old World monkeys. For example, Japanese (*Macaca fuscata*) and pigtail (*Macaca nemestrina*) macaques not only associate preferentially with kin, but, within the kin class, also form alliances more often with close relatives like siblings than with more distantly related individuals like nieces or nephews (*7, 36*). As noted above, field experiments show that rhesus macaques use vocalizations to communicate about their dominance and kin relations with current opponents.

In similar experiments on free-ranging vervet monkeys, the scream of a 2-year-old juvenile was played from a concealed loudspeaker to three adult females, one of whom was the juvenile's mother. As expected, mothers responded more strongly than other females, indicating that they recognized the screams of their offspring. The other females, however, responded to playbacks by looking at the mother, often before the mother herself had responded (*37*). Females behaved as if they were able to associate particular screams with particular juveniles, and these juveniles with particular adult females, suggesting that monkeys not only distinguish their own offspring from others, but also recognize the associations that exist among other group members. We cannot yet, however, rule out the possibility that these results simply reflect a learned association between the screams of a particular juvenile and reliable and dramatic behavioral responses by the mother (*31*).

Studies of baboons provide further evidence that monkeys may recognize the social relations of others and that such recognition is not limited to bonds among kin. In the wild, adult male hamadryas and gelada baboons challenge the resident male of one-male multi-female units in attempts to take over his position (*38*). Take-over attempts occur less often and are less likely to succeed if close bonds (for example, frequent grooming) exist between the resident male and his females. Experiments have shown that among hamadryas baboons a male is less likely to challenge another if the latter is with a female that strongly prefers him (*39*). Similarly, male savannah baboons are less likely to challenge a consortship if the male and his partner have a long-term friendship (*14*). The apparent recognition of close, as opposed to weakly bonded, social relationships therefore seems to inhibit challenges even when, under other circumstances, the challenger dominates his rival (*14, 39*).

Chimpanzees also appear to recognize other individuals' social relationships. For example, chimpanzees reconcile after fights by kissing one another (*29*). Such reconciliations seem to be particularly important among adult males, but when male dominance relationships are unstable, each male exhibits reluctance to be the one to initiate the friendly contact. When this occurs, a third party, often an adult female, sometimes initiates a reconciliation by leading one individual to his opponent. Females benefit from the reconciliation because tense males often attack females and offspring (*18*).

Female-initiated reconciliations indicate not only that primates perceive relations between others, but that they can use this knowledge for their own apparent benefit. Observations of redirected aggression support this suggestion. When aggression is directed at a baboon or macaque by a higher ranking opponent, the victim frequently redirects aggression onto an innocent bystander. More often than expected by chance, the targets of such redirected aggression are "friends" or relatives of the original aggressor (*14, 40*). Similarly, vervet monkeys of all ages behave aggressively toward another individual more often when they have recently fought with that individual's close matrilineal kin (*41*). Adult vervets also exhibit a more complex form of redirected aggression: an individual is significantly more likely to threaten a particular animal if that animal's kin and one of its own kin fought earlier that same day (*41*). This result holds only for animals more than 3 years of age, suggesting that it takes time for younger monkeys to learn the complexities of the social network.

Whatever the developmental mechanism, the vervet data suggest (but by no means prove) that adult primates not only recognize the close associates of other animals but also recognize that certain sorts of relationships share similar characteristics, regardless of the particular individuals involved. If this latter observation were confirmed, it would indicate that primates, in their recognition of social alliances, solve problems that are functionally equivalent to laboratory tests of analogical reasoning.

Goals and Attribution

The behavior of primates often gives the impression of intentional striving toward a conscious goal (*18*). Although systematic laboratory experiments have documented the existence of such mental processes in captive chimpanzees (*33*), most attempts to do so in natural social groups rest on the compilation of anecdotes that are difficult to explain without ascribing intention to the individuals involved. Although such anecdotes clearly lack many crucial controls, they are sufficiently compelling to suggest that additional research and experiments are warranted. Several examples are given below.

Kummer (*35*) observed hamadryas baboons on the steep, rocky cliffs where they sleep. An adult male sat on a ledge, watching two juveniles playing on the ledge below. Suddenly a rock became dislodged near the male and began to fall toward the juveniles. The male grabbed the rock and held it in place. A few minutes later, when the juveniles had moved away, the male let the rock fall to the ground.

Behavior apparently directed toward a goal removed from the immediate context also constitutes indirect evidence for conscious planning. For example, wild chimpanzees use vegetation to make tools suitable for fishing termites out of mounds. On many occasions, observers have watched a chimpanzee make such a tool and then carry it around for several minutes while searching for an appropriate termite mound. Similar planning also seems to occur in the social realm. Chimpanzee males regularly form large parties that patrol the boundaries of their community range in search of chimpanzees from neighboring communities (*21*). One of us (B.S.) once observed Figan, an alpha male who had been traveling alone for a few days, wake up in the morning and move rapidly through the forest until he located first one male associate and then another. In each case, he groomed the male briefly and then led him away in search of others. When he had collected several males, Figan silently led the party into a neighboring territory where they attacked three animals who were isolated from other members of their community.

Observations of apparent deception are also suggestive of planning and foresight. For example, at the Gombe Stream reserve in Tanzania, chimpanzees were at one time provisioned with bananas by researchers. On one occasion, an adolescent male, Figan, was unable to obtain many bananas because of competition from other group members. Suddenly, Figan walked out of the provisioning area in a manner that caused all others nearby to follow him. Shortly thereafter he abandoned his companions, circled back, and ate the remaining bananas by himself. Figan repeated this maneuver many times (*42*). DeWaal (*18, 43*) and Menzel (*44*) report many similar instances of deceptive behavior among captive chimpanzees.

Deception appears not to be limited to great apes. Wild baboons have been observed to employ routine vocalizations and gestures in novel contexts in apparent attempts to deceive others about their own motives or intentions (*45*). Similarly, both field observations and experiments on vervet monkeys have suggested that individuals may adjust their rate of alarm calling to alert kin to the presence of predators and to withhold such information from nonkin and potential rivals (*46*).

Although nonhuman primates may have intentions, it is difficult to determine whether they attribute such intentions to others and act on the basis of such attributions or are reacting to some other, simpler cue. For example, in a captive group of chimpanzees (*18*), two adult males, Luit and Nikki, were engaged in a prolonged struggle for dominance. During one fight Nikki was driven into a tree. As Luit sat at the bottom of the tree, he nervously "fear grinned." He then turned away from Nikki, put his hand over his mouth and pressed his lips together, apparently to hide this sign of submission. Only after the third attempt, when Luit succeeded in wiping the fear grin from his face, did he once again turn around to face Nikki. Luit's actions suggest that he was aware of his own nervousness, of the external manifestation of his fear, and of the need to hide his fear from his rival. It is tempting to speculate that Luit was indeed attributing motives to Nikki, but until definitive experiments are designed to test this hypothesis, simpler explanations are also possible.

Social and Nonsocial Knowledge

Primates tested in the laboratory with objects often face problems that are logically similar to the social problems confronted by primates in the wild. Despite this similarity, primate performance in these two contexts often differs strikingly. For example, while transitive inference has been documented in both captive squirrel monkeys and chimpanzees (*47*), this ability emerged only after considerable training with paired stimuli. In contrast, field observations suggest that monkeys readily deduce a dominance hierarchy among conspecifics through observation of paired interactions (*48*). Moreover, as described above, examples from the field suggest that primates can predict the consequences of their behavior for others and that they understand enough about the motives of others to be capable of deceit and other subtle forms of manipulation (*14, 18, 41–46, 49*). Such observations are both intriguing and frustrating, because they suggest the existence in the wild of striking mental abilities that are less easily demonstrated in the laboratory.

One possible explanation for the differing performance of primates in the field and laboratory is that selection for intelligence has acted particularly strongly in the social domain. This argument suggests that during primate evolution group life exerted strong selective pressure on the ability to form complex associations, reason by analogy, make transitive inferences, and predict the behavior of fellow group members. Thus when captive chimpanzees solve technological problems that require foresight and an understanding of the consequences of past decisions (*33, 50*), they may be demonstrating abilities for which they have been preadapted as a result of the need to make equally strategic decisions about each other (*18, 34, 51*). Such a domain-specific hypothesis specifies the selective factors that originally gave rise to intelligence; it does not claim that social knowledge can never be extended to other spheres, nor does it make any claims about the mechanisms, cognitive or otherwise, underlying performance.

The proposal that natural selection has acted to favor abilities particularly useful in interactions with conspecifics can be tested only by presenting individuals with logically similar problems, some of which involve conspecifics and others of which involve inanimate objects or other species. Thus far, few such tests have been performed, although preliminary field experiments have been conducted on vervet monkeys. Results suggest that vervets perform better on tests that use social, rather than nonsocial, stimuli. For example, although vervets appear to recognize with which ranges the members of other vervet groups are associated, they seem not to recognize the ranging patterns of other species. When researchers play the calls of species that are habitually found near water, vervets respond similarly regardless of whether the speakers are near waterholes or in arid woodlands (*52*). Similarly, while in their social interactions vervets seem able to learn complex associations involving other individuals, outside the social domain they appear not to have formed associations between, for example, a leopard and a gazelle carcass left in a tree or a python and its fresh track left in the dirt (*52*).

Furthermore, although monkeys and apes often exchange grooming, alliances, and tolerance at food sites, such cooperation rarely involves the use or exchange of objects. Nonhuman primate tool use, which has received considerable attention because of its relevance to human evolution, is striking in part because it is relatively rare. By comparison, primatologists repeatedly emphasize the ability of the subjects to use other individuals as "social tools" to achieve particular results (*14, 18, 28, 38*). Moreover, although parties of baboons and chimpanzees often hunt and kill prey, little evidence indicates that such hunts are truly cooperative or that animals genuinely share meat (*53*). Social interactions in some nonprimate animals (for example, the courtship displays of many birds) occasionally involve exchange of material goods. What we do not know, however, is whether such patterns of exchange are at all modifiable. While humans readily exchange a behavioral altruistic act for a material one, such flexibility in the "currency" of reciprocal acts has seldom been convincingly documented in other animals. As indicated in the experiments with vervet monkeys cited earlier, however, nonhuman primates appear to trade acts in one social currency (such as grooming) for acts in another social currency (such as alliances) (*26*).

Some researchers have argued that ecological pressures have played a major role in the evolution of primate intelligence (*54*). This proposal emphasizes the limits of the distinction that we have drawn between social and nonsocial knowledge. For example, primate memory may have evolved as a result of the need to remember both the location of spatially dispersed food resources and previous social encounters. Indeed, the challenge of exploiting dispersed and ephemeral food items may select for increased intelligence not simply because food collection itself becomes more difficult, but also because ecological complexity sets the stage for increasingly complex social competition.

At the same time, it is unclear at present whether ecological variables alone can explain the intricacies of intragroup behavior among primates. For example, in both mountain gorillas and Burchell's zebras (*Equus burchelli*), females disperse from their natal groups to live with a single dominant male and a number of unrelated females. Since both species also feed on evenly distributed and widely abundant food, it is tempting to hypothesize that each species' mating system has evolved in response to similar selective pressures exerted by similar ecological factors. Behavior within gorilla groups, however, is characterized by a complexity of social interactions (*55*) that seems unmatched by zebras. The factors that might have given rise to these interspecific differences are still far from understood.

For the future, a range of questions remain to be studied. We need to compare the complexity of social interactions, both between primates and other animal groups and across different primate species. We must investigate the extent to which problem-solving abilities manifested in the laboratory resemble those used in naturally occurring social situations, and, if so, whether we might eventually be able to use performances on laboratory tests to predict qualitative differences in social relationships across species. Finally, field research should focus on primates' knowledge of their physical environment in addition to their social relationships. This is essential if we are to compare social intelligence with intelligence in other domains, and if we are to test the intriguing hypothesis that primate intelligence—including our own—originally evolved to solve the challenges of interacting with one another.

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Research Articles

A Deletion Truncating the Gonadotropin-Releasing Hormone Gene Is Responsible for Hypogonadism in the *hpg* Mouse

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Hereditary hypogonadism in the hypogonadal (*hpg*) mouse is caused by a deletional mutation of at least 33.5 kilobases encompassing the distal half of the gene for the common biosynthetic precursor of gonadotropin-releasing hormone (GnRH) and GnRH-associated peptide (GAP). The partially deleted gene is transcriptionally active as revealed by in situ hybridization histochemistry of *hpg* hypothalamic tissue sections, but immunocytochemical analysis failed to show the presence of antigen corresponding to any part of the precursor protein.

THE CENTRAL REGULATION OF REPRODUCTIVE COMPETENCE in mammals is mediated by the activity of hypothalamic neurons and relies on the correct expression of a single distinguishing gene that encodes the precursor protein for the decapeptide GnRH (gonadotropin-releasing hormone) and the 56–amino acid peptide GAP (GnRH-associated peptide) (*1, 2*). These biosynthetically linked hypophysiotropic peptides are released at intervals into the portal circulation where they stimulate the pulsatile release of gonadotropins and suppress prolactin secretion from the anterior pituitary (*1–3*). Failure in this system may lead to the common reproductive disorder of hypogonadism, which is often associated with hyperprolactinemia (*4*).

The hypogonadal (*hpg*) mouse, first described in 1977 (*5*), is an appropriate animal model to study this disorder. In this mouse, an isolated deficiency in pituitary gonadotropin secretion leading to a failure of testes and ovaries to develop postnatally is genetically linked to an autosomal recessive mutation. The primary genetic lesion seems to lie within the structural gene for GnRH or in a gene or genes required for its correct expression since GnRH cannot be detected in *hpg* mouse brain, although *hpg* mouse pituitary gonadotrophs are responsive to the decapeptide (*6*). Phenotypic reversal of the *hpg* disorder was achieved by grafts from preoptic parts of the normal fetal brain, which restored functional GnRH- (and presumably GAP-) secreting hypothalamic neurons (*7*).

To determine whether and how the GnRH gene is altered in the *hpg* mouse, we isolated this gene locus from normal and *hpg* mice. Detailed analysis revealed a deletion in the *hpg* genome of at least 33.5 kilobases (kb); this deletion removed the two GnRH gene exons that encode most of the GAP peptide, resulting in a transcriptionally active, but translationally incompetent, truncated gene.

The GnRH-GAP gene from mouse. To provide a basis for comparison of the GnRH gene in normal and *hpg* animals, we isolated the cloned normal gene and delineated its structure. The map of this gene locus and the complete nucleotide sequence of the gene are shown in Figs. 1 and 2. Exon-intron boundaries were assigned on the basis of homologous rat hypothalamic complementary DNA (cDNA) sequences (*8*). The distribution of exons shows close homology of the mouse gene to the corresponding human and rat genes (*8*). The three coding exons (II, III, and IV) encode amino acids 1 to 45, 46 to 77, and 78 to 90, respectively, of the GnRH-GAP precursor. The sequence of the mouse precursor, 90 amino

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