

Sex Differences in Play Among Western Lowland Gorilla (*Gorilla gorilla gorilla*) Infants: Implications for Adult Behavior and Social Structure

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ABSTRACT Mammalian play is believed to improve motor skills as well as facilitate the development of social relationships. Given the marked sexual dimorphism in gorilla body size and the role assumed by the male in protecting the group from conspecifics and predators, the motor-training hypothesis of play predicts that male infants should exhibit higher frequencies of social play than female infants, and that males should prefer to play with other males. Given that adult female gorillas are strongly attracted to adult breeding males and form only weak social bonds with unrelated adult females, the social-relationship hypothesis of play predicts that female infants should prefer to play with males. These hypotheses were

tested in a 22-month study of 12 gorilla infants, aged between 0–5 years, living in three zoological parks in Chicago and Atlanta. Consistent with the hypotheses, male infants played more than female infants did, and both male and female infants preferred to play with males rather than with females. These findings suggest that sex differences in play in the great apes and other primates can be predicted by the characteristics of adult behavior and social structure above and beyond the patterns of sex-biased dispersal or coalition formation with same-sex kin. *Am J Phys Anthropol* 123:52–61, 2004.

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Play is widespread in mammals, and has also been reported in birds and a few reptiles (Fagen, 1981; Bekoff and Byers, 1998). Play may be a non-functional activity, or it may play an important role in sensory, motor, social, and cognitive development (e.g., Fagen 1981, 1993; Spinka et al., 2001).

One possible function of play is to allow individuals to practice and perfect those motor skills that might later be used for capturing prey, avoiding predators, fighting with conspecifics, attracting a mate, or taking care of infants (e.g., Fagen, 1981; Smith, 1982; for further discussion of this “motor-training hypothesis,” see Byers and Walker, 1995; Spinka et al., 2001). Another possible function of play is to facilitate the development and negotiation of relationships with individuals with whom the immature will associate as an adult. According to this “social-relationship hypothesis,” by playing frequently with individuals of particular age, sex, or kinship classes, developing animals may learn the behavioral characteristics of these individuals and form bonds with them that may be useful later in life (e.g., Baldwin and Baldwin, 1974; Nakamichi, 1989; Fairbanks, 1993).

Sex differences in play are expected to occur whenever males and females in any given species differ in their physical characteristics (e.g., body size or weaponry), behavioral characteristics (e.g., differential involvement in activities such as hunting,

predator avoidance, intraspecific fighting, tool use, or infant caretaking), or social preferences (e.g., the formation of strong bonds with same-sex vs. opposite-sex individuals, or with kin vs. nonkin). In these circumstances, the motor-training and the social-relationship hypotheses predict sex differences in both the frequency/type of play and in play-partner preferences, although these predictions are not necessarily mutually exclusive. Unfortunately, there have been only a few tests of these hypotheses, particularly with comparative data from different mammalian species (but see Pellis and Iwaniuk, 2000).

Among nonhuman primates, sex differences in frequency of play, type of play, and play-partner preferences have been best documented in cercopithecine monkeys, and in particular, in macaques and baboons (e.g., Fagen, 1993). In these primates,

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males are generally larger and have larger canines than females, and compete aggressively with each other for access to mating partners (e.g., Melnick and Pearl, 1987). Furthermore, males are typically the dispersing sex, and females the philopatric sex (e.g., Melnick and Pearl, 1987). This implies that females typically form strong social bonds and alliances with their female relatives in their natal groups, whereas males have to negotiate alliances and dominance relationships with unrelated adults in the group to which they immigrate.

In macaques and baboons, infant and juvenile males typically play more often and more vigorously than females do (e.g., macaques: Hinde and Spencer-Booth, 1967; Fady, 1976; Symons, 1978; Eaton et al., 1985, 1986; Glick et al., 1986; Koyama, 1985; baboons: Kummer, 1968; Owens, 1975; Cheney, 1978; Chalmers, 1980; Young et al., 1982; Pereira, 1984). Macaque immatures typically play with individuals of the same sex and age (e.g., Fady, 1976; Glick et al., 1986; Ehardt and Bernstein, 1987). Juvenile males also play with subadult and adult males, whereas juvenile females engage in more solitary play and more infant handling than males do at any age (e.g., Kuyk et al., 1977; Symons, 1978; Ehardt and Bernstein, 1987; Lovejoy and Wallen, 1988). The sex differences in cercopithecine play are generally consistent with the motor-training hypothesis of play. The high frequency of male-male play may also be consistent with the social-relationship hypothesis of play, because competitive and cooperative interactions with other males may have an important effect on male reproductive success. However, given that cercopithecine females form strong social bonds with other females, the social-relationship hypothesis would predict much greater levels of female-female play than are actually observed. Instead, it seems that cercopithecine females develop bonds with other females mostly through grooming rather than play (e.g., Dunbar, 1991).

Play behavior and its relationship to the species' morphological, behavioral, and social characteristics are less well-known in the great apes (Fagen, 1993). Chimpanzees, bonobos, orangutans, and gorillas differ from one another in many respects, including the degree of sexual dimorphism in body size, social organization, patterns of sex-biased dispersal, and male and female involvement in intragroup fighting, hunting, or intergroup encounters (McGrew et al., 1996). In chimpanzees and bonobos, the facts that sexual dimorphism in body size is minimal, and that male reproductive success depends less on intrinsic power than in the other species, might predict few or no sex differences in social play (Watts and Pusey, 1993). In chimpanzees, however, males are involved in both conspecific fighting and hunting more than females are (Nishida and Hiraiwa-Hasegawa, 1987). Furthermore, unlike females, chimpanzee males tend to remain in their natal groups and form coalitions with kin of the same sex (Nishida and Hiraiwa-Hasegawa, 1987). Based on these character-

istics, it may be argued that chimpanzee males should play more than females, and mostly with other males. In bonobos, on the other hand, female dominance and female-female coalitions (Kano, 1992) would predict that females play more than males, and mostly with other females. In orangutans and gorillas, the facts that males are larger than females, and that male reproductive success depends to a large extent on intrinsic power (Watts, 1996), would predict that males should play more than females, and mostly with other males. The social organization of orangutans is still poorly understood (Singleton and van Schaik, 2002), and therefore, the implications of the social-relationship hypothesis of play for this species are unclear. As for gorillas, Brown (1988) argued that sex differences in play might not be expected in a species where both males and females transfer from their natal group and do not form strong bonds with kin of the same sex. It may be argued, however, that given the male-centered nature of gorilla groups, both males and females should be interested in forming relationships with males and therefore play with them, whereas females should have little interest in playing with other females. Male-male play should also be favored by the fact that males may spend part of the lives in all-male groups (Watts, 1996).

The research on play in the great apes is somewhat limited and difficult to interpret. In chimpanzees, sex differences in play similar to those observed in cercopithecines have been consistently reported by studies conducted in captivity (e.g., Nadler et al., 1987; Mendoza-Granados and Sommer, 1995; Spijkerman et al., 1996) but not in the wild (Hayaki, 1985; Goodall, 1986; Pusey, 1990). Unfortunately, there are very few studies of play in bonobos, and virtually no data on sex differences (e.g., Enomoto, 1990; Kano, 1992). In orangutans, Rijksen (1978) reported that immature male-male play was more frequent and longer than male-female or female-female play. Adolescent females played more with males than with females, but males responded more to other males. Orangutan play has also been studied in captivity, but there are few or no data on sex differences (Nadler and Braggio, 1974; Zucker et al., 1986; Poole, 1987). Among wild mountain gorillas, Fossey (1979) and Watts and Pusey (1993) reported few observations suggestive of sex differences in play, whereas among captive western lowland gorillas, Brown (1988) reported no significant sex differences in the frequency of social play or the type of play among juveniles, subadults, and adults. She did report, however, that male-male play dyads and male-female dyads were common, whereas females rarely played with other females, suggesting a possible sex difference in play-partner preferences (for a similar finding, see Freeman and Alcock, 1973; Fischer and Nadler, 1978). When taken together, the data available on play in the great apes are insufficient for a comprehensive test of the motor-training and social-relationship hypotheses. More data on

play are needed for all four species of great apes, both in captivity and in the field.

The goal of this study was to test some of the predictions of the motor-training and social-relationship hypotheses of play in captive western lowland gorillas. The social organization of western lowland gorillas is not well-known, but sex differences in life history are generally comparable to those documented for mountain gorillas (Watts, 1996; Goldsmith, 1999). The motor-training hypothesis predicts that immature males should engage in social play more frequently than females do, and that males should play mostly with other males because they provide the best training partners. Different aspects of the social-relationship hypothesis make contrasting predictions about sex differences in play-partner preferences. If the crucial factor for play-partner preferences is sex-biased dispersal and the opportunity to form alliances with same-sex kin, then sex differences in partner preferences are not necessarily expected. However, if attraction to adult males is the main factor governing gorilla social relationships regardless of patterns of dispersal and alliances with kin, then males are expected to be the preferred play partners of both males and females. Since relationships between adult males and females are an important component of gorilla social structure (Watts, 1992), immature males should also show some interest in initiating playing with females, or at least in reciprocating social play with them. In contrast, immature females should have little interest in playing with each other. In addition to exploring sex differences in play among infant gorillas, we also aimed at describing the development of different forms of play over the first 5 years of life. Such developmental changes may provide useful information about the functional significance of play for adult behavior and social structure. Finally, we also investigated whether mothers actively encouraged or discouraged the play behavior, or more generally, the social activities of their infants. Selective maternal encouragement or discouragement of play may be one possible mechanism through which sex differences in infant play originate or are reinforced.

METHODS

Subjects and housing

Study subjects were 12 western lowland gorilla infants housed in three different zoological parks. Six infants were housed at Zoo Atlanta (Atlanta, GA), 5 infants at Lincoln Park Zoo (Chicago, IL), and 1 infant at Brookfield Zoo (Chicago, IL). Six infants were male, and 6 were female. Infant ages during the study ranged between 0–63 months. All infants were mother-reared, although two infants at Lincoln Park Zoo and one at Zoo Atlanta were reared by a surrogate mother. Preliminary analyses showed that the surrogate-reared infants did not differ significantly from the mother-reared infants in any of

the behavioral measures considered in this study. The gorillas in Atlanta lived in two social groups housed in outdoor, naturalistic enclosures of approximately 22,600 square feet. The exhibits contained grass substrate, as well as trees, bushes, and rock outcroppings. Animals were fed four meals a day: a morning and evening feeding of monkey chow, and a morning and afternoon feeding of fruits and vegetables. The group at Lincoln Park Zoo was housed indoors in an area of approximately 1,000 square feet. The area contained a variety of climbing structures, including ropes, nets, and “metal trees,” and ranged in height from 20–27 feet. Fresh hay was the primary substrate, and skylights provided fresh air and sunlight in favorable weather conditions. Animals were fed twice daily by scattering chow, fruit, and vegetables throughout the exhibit. The group at Brookfield Zoo was housed in a large indoor exhibit of approximately 6,400 square feet with a rocky substrate and several trees and other climbing structures. Animals were fed 2–3 times a day with chow and fruit or vegetables. Table 1 presents information on the composition of the gorilla groups in Chicago and in Atlanta.

Procedure

Eleven infants were observed once a week in 60-min focal observation sessions for 22 months, beginning in January 2000. In total, about 90 hr of observation per infant were made. The infant at Brookfield Zoo was born during the second year of the study and observed for only 7 months. Data for this infant were only used to describe early developmental changes in behavior, but not sex differences in play. Data were collected by different observers in Atlanta and Chicago, after reliability tests showed at least a 90% agreement between observers. Observations were made between 9:00–17:00 hr, and the order in which subjects were observed was randomized.

The days of the week in which subjects were observed were also randomized, and all observations were made while they were on exhibit. All subjects were habituated to the presence of zoo visitors and observers, and showed little interest in them during the observation periods.

Data on play were collected with a check sheet and a tape recorder, using the focal sampling technique. Solitary locomotor play was recorded whenever an infant was observed running, climbing, or jumping without interacting with conspecifics. Solitary object play was defined as an infant manipulating an object without using it for any obvious purpose. Social play was recorded when two or more individuals chased and wrestled with each other. A new bout was scored after a 10-sec pause in play and play-related activities. The following behavior patterns were also recorded: play face (a facial expression in which the mouth is wide open without showing teeth, as if attempting to bite), mockbite (an interaction in which an individual holds another individ-

TABLE 1. Group composition in Chicago and Atlanta with information on sex and age (at the beginning of study) of all individuals¹

Chicago					
Lincoln Park Zoo			Brookfield Zoo		
Name	Sex	Age	Name	Sex	Age
Frank	M	36 years	Ramar	M	32 years
Debbie	F	34 years	Alpha	F	39 years
Makari	F	13 years	Babs	F	26 years
Bulera	F	11 years	Binti	F	12 years
Bahati	F	10 years	Baraka	F	10 years
Tabibu	F	8 years	Koola	F	5 years
Madini	F	42 months	Nadaya	M	0 months
Rollie	F	38 months			
Jelani	M	35 months			
Mumbali	F	24 months			
Bengati	M	18 months			

Atlanta					
Zoo Atlanta group 1			Zoo Atlanta group 2		
Name	Sex	Age	Name	Sex	Age
Willie B	M	41 years ²	Ozoum	M	39 years
Choomba	F	37 years	Katoomba	F	38 years
Machi	F	24 years	Paki	F	37 years
Kuchi	F	16 years	Banga	F	36 years
Mia	F	11 years	Charlie	M	42 months
Kudzoo	F	6 years	Jasiri	M	18 months
Kashata	F	7 years			
Olympia	F	42 months			
Kidogo	M	20 months			
Sukari	F	19 months			
Lulu	F	2 months			

¹ F, female; M, male.

² Willie B. died shortly after beginning of study.

ual's body part in its mouth for a few seconds without clenching its teeth), display (chest-beating or shaking the cage walls), and clap/drum (clapping hands or drumming on the floor or other substrate). Finally, the focal sampling technique and the tape recorder were used to record any forms of maternal encouragement or discouragement of infant social behavior. Maternal encouragement of social interaction included any attempts by the mother to encourage interactions between the infant and other individuals, e.g., by placing the infant in close proximity to another infant and encouraging play. Discouragement included events in which the mother interrupted a play bout between the infant and another individual and/or pulled the infant away from another individual. A detailed description of measures of maternal encouragement and discouragement, along with a description of other measures of mother-infant interactions and infant social and nonsocial activities not included in this study, can be found in Maestripietri et al. (2002).

Data analyses

Possible significant differences in infant sex or mother's parity between the Atlanta and Chicago dyads were analyzed with Fisher's exact probability test. Infant age and mother's age were compared with Student's *t*-tests. Sex differences in behavioral measures were assessed with *t*-tests for unpaired samples. Correlations were assessed with Pearson's correlation coefficient. Play-partner preferences

were analyzed with repeated-measures ANOVA followed by Bonferroni-Dunn post hoc tests. To compare male and female preferences for same-sex vs. opposite-sex play partners, we used two-way ANOVAs. Whenever the data were nonnormally distributed or the variances were nonhomogeneous, we analyzed log transformations of the data. All tests were two-tailed, and $P \leq 0.05$ was considered statistically significant.

RESULTS

The 6 Atlanta mother-infant dyads did not differ significantly from the 6 Chicago dyads in terms of infant sex, mother's age, or mother's parity. There were no significant differences between the two locations in any of the behavioral measures considered in this study.

Sex differences and development of play

As shown in Figure 1, males scored higher than females in all frequency measures of play and play-related activities, including solitary locomotor play, solitary object play, social play, play face, mockbite, display, and clap/drum. Sex differences were statistically significant for initiation of social play ($t_9 = 2.59, P < 0.05$), play faces shown by infants ($t_9 = 2.45, P < 0.05$), and displays ($t_9 = 2.93, P = 0.01$). The infant born at Brookfield Zoo was excluded from these statistical analyses because he was too young to engage in most active forms of play.

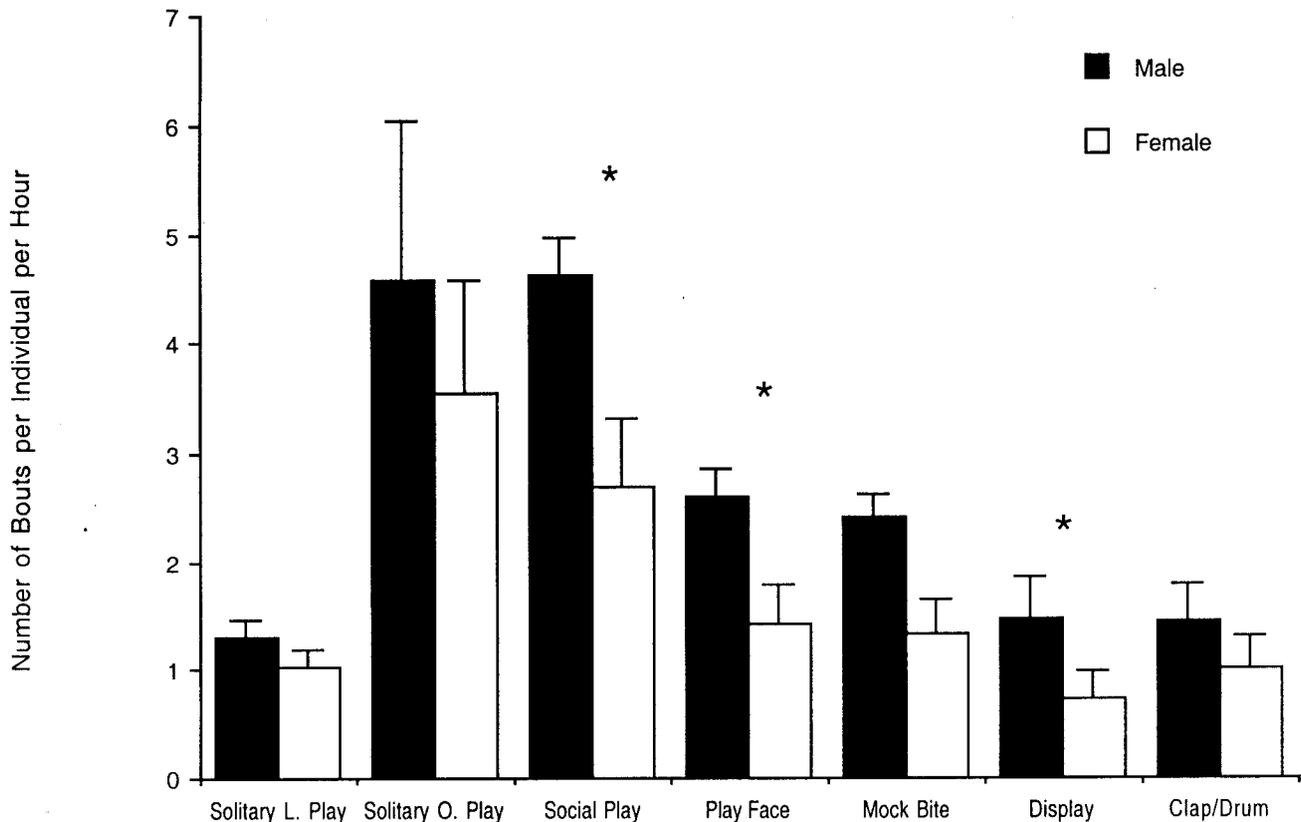


Fig. 1. Mean (\pm SEM) number of play bouts per hour per individual for males and females, and different categories of play and play-related behaviors.

To describe the developmental changes in the three main types of play, the data for solitary locomotor play, solitary object play, and social play were grouped into 10 6-month age periods: 1–6 ($N = 2$), 7–12 ($N = 2$), 13–18 ($N = 3$), 19–24 ($N = 6$), 25–30 ($N = 5$), 31–36 ($N = 6$), 37–42 ($N = 9$), 43–48 ($N = 6$), 49–54 ($N = 5$), and 55–60 months ($N = 5$). All forms of play increased in the first 2 years of life (Fig. 2). Solitary locomotor play declined steadily after the second year. Solitary object play and social play were more frequent than solitary locomotor play, and both continued to increase into the third year and declined thereafter. Figure 2 only shows the frequency of social play initiated by the focal infants. The total frequency of social play (both initiated by the focal infants and by other individuals) was approximately twice as high. Thus, from the second year of life onward, social play was the most common form of play. The developmental changes in play faces, mockbites, and displays were approximately similar to those observed for social play (data not shown).

There was a significant positive correlation between solitary locomotor play and initiation of social play ($r = 0.78$, $N = 11$, $P < 0.01$). In contrast, there was no significant correlation between solitary object play and social play, or between solitary object play and social play. Initiating social play was positively correlated with receiving social play ($r =$

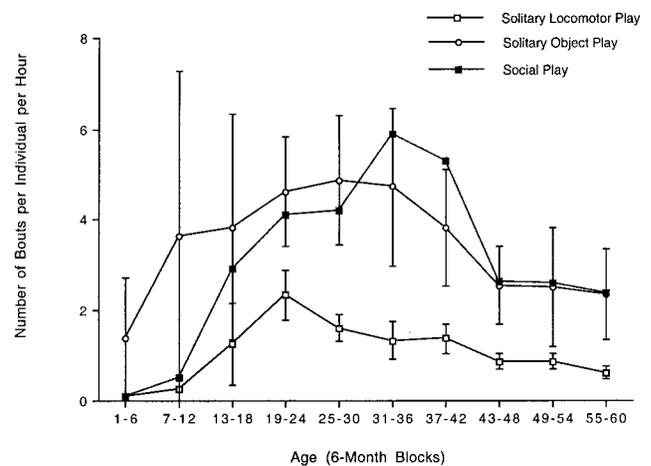


Fig. 2. Time course of three types of play in infant gorillas over first 5 years of life (6-month blocks). Data are presented in terms of mean (\pm SEM) number of play bouts per hour per individual. See text for information on sample size in each age period.

0.69, $N = 11$, $P = 0.01$), suggesting that this is a highly reciprocal activity (see below).

Play faces and mockbites done and received were positively correlated with each other as well as with social play initiated and received. Clap/drum was positively correlated with the initiation of social play

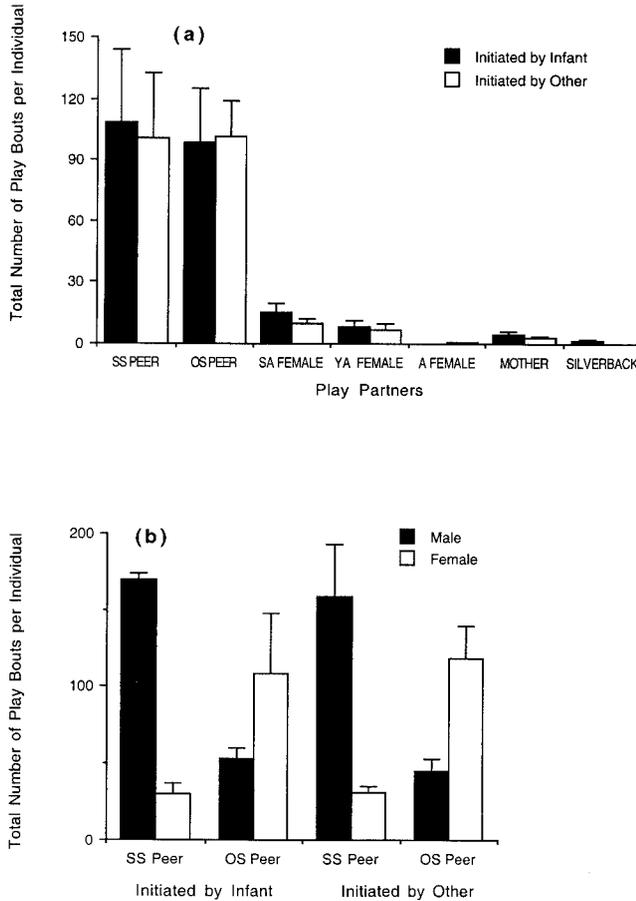


Fig. 3. a: Total number of social play bouts initiated by focal infants or other individuals (mean \pm SEM per individual) for different categories of individuals. SS PEER, same-sex peer; OS PEER, opposite-sex peer; SA FEMALE, subadult female (6–8 years); YA FEMALE, young-adult female (10–16 years); A FEMALE, adult female (>20 years). b: Total number of social play bouts initiated by focal infants or other individuals (mean \pm SEM per individual) for males and females with same-sex (SS) or opposite-sex (OS) peers.

($r = 0.65$, $N = 11$, $P < 0.05$), but not with play initiated by others or with play faces or mockbites.

Displays were not significantly correlated with the frequency of social play, or with play faces or mockbites.

Play-partner preferences

Figure 3a shows the identity of all play partners when play was initiated by the focal infant and by other individuals. Only 3 infants had access to all seven classes of play partners. A repeated-measures ANOVA conducted with these 3 subjects revealed an overall significant difference between the seven categories of play partners (initiated by infant: $F_{2,6} = 4.31$, $P = 0.01$; initiated by other: $F_{2,6} = 5.63$, $P < 0.01$), with play with same-sex or opposite-sex peers being more frequent than play with other categories of individuals ($P < 0.05$ for all post hoc tests).

Eight infants had access to both same-sex and opposite-sex peers within their groups. When the

partner preferences of these 8 infants were analyzed, a significant interaction emerged between the sex of the focal infant and the sex of its preferred play partners (initiated by infant: $F_{1,6} = 11.1$, $P = 0.01$; initiated by other: $F_{1,6} = 23.57$, $P < 0.01$), such that male infants mostly played with peers of the same sex, whereas females mostly played with peers of the opposite sex (Fig. 3b). In other words, both males and females preferred to play with males. Infant males showed a tendency to play with subadult females more than females did (male = 25.67 ± 8.45 ; female = 10.33 ± 3.21 , $t_9 = 2.11$, $P = 0.07$) and a similar frequency of play with their mothers (male = 4.80 ± 2.78 ; female = 4.17 ± 1.90). Only males initiated play with adult females other than their mother or with the silverback.

All 17 possible infant-infant dyads engaged in social play. There was a strong positive correlation between the number of play bouts initiated by both individuals in a dyad ($r = 0.91$, $N = 17$, $P = 0.0001$). Of the 55 possible infant-adult female dyads, 38 exchanged social play. Again, there was a significant correlation between the number of play bouts initiated by the infant and those initiated by the adult female within dyads ($r = 0.75$, $N = 38$, $P = 0.0001$). The correlation was still significant if the infants' mothers were excluded from the analysis. Thus, although there were marked differences in the frequency with which individuals or dyads engaged in social play, within dyads, play was a highly reciprocal activity. When infants played with older females, there was no significant difference between the number of play bouts initiated by infants and those initiated by older females. The same result was found also without the infants' mothers in the analysis.

Maternal influences on infant social play

Mothers appeared to play little or no role in the play activities or play-partner preferences of their offspring. Mothers were never observed to encourage their infants to engage in play or any other social activities with other individuals. There were 18 observations of maternal discouragement of infant social interactions, 10 of which occurred in the context of play. Maternal discouragement of infant social interaction was negatively correlated with infant age at the beginning of the study ($r = 0.75$, $N = 11$, $P < 0.01$). Thus, younger infants were discouraged more than older infants. There were no significant sex differences in maternal discouragement of infant social interactions.

DISCUSSION

Western lowland gorilla infants aged between 0–5 years showed sex differences in the initiation of social play, play faces, and displays, with males exhibiting these activities significantly more often than females did. There was also a clear sex difference in the initiation of play with same-sex vs. opposite-sex

peers, with male peers being the preferred play partners of both male and female infants. Although we cannot establish whether differences in the frequencies of play were accompanied by similar differences in total duration or bout length, it is reasonable to argue that information on the frequency of initiation is a good indicator of overall tendency to play and of play-partner preferences.

The findings of this study are similar to those reported for captive chimpanzees (e.g., Mendoza-Granados and Sommer, 1995), but are difficult to compare to those of previous studies of gorilla play. Previous studies of play in western lowland gorilla infants had very small sample sizes (e.g., $N = 3$, Hoff et al., 1981) or larger sample sizes but also methodological complications (e.g., in Meder (1990), most infants had been hand-reared and housed in pairs). Brown (1988) had a large sample size and reported no sex differences in frequency or type of play. However, in Brown (1988), 14 of 19 individuals were in the age range of 7–26 years, and therefore there were only a few infants. Finally, field studies of mountain gorillas made no systematic attempts at investigating sex differences in play (e.g., Schaller, 1963; Fossey, 1979; Dixon, 1981; Watts and Pusey, 1993). Although data collected in captivity and in the field may be difficult to compare in terms of frequencies of behavior and context of occurrence, the age- and sex-related differences in play observed in the three captive environments of this study should be generalizable also to other settings.

The sex differences in social play among infant gorillas are consistent with the prediction of the motor-training hypothesis. Gorilla males are larger than females and play an active role in protecting their group from external threats, and their reproductive success is in large part dependent on their intrinsic power rather than on coalitions with conspecifics (e.g., Watts, 1996). These characteristics suggest that male immatures should practice their fighting skills through wrestle and chase play, and that their best training partners are likely to be other males (e.g., Fagen, 1981). The observed sex difference in social play contradicts one possible interpretation of the social-relationship hypothesis, according to which sex differences should not be expected in species in which both sexes disperse from their natal group and individuals do not form coalitions with same-sex kin (e.g., Brown, 1988; Mendoza-Granados and Sommer, 1995). Sex-biased dispersal and coalition formation with kin, however, are only two of many socioecological variables that affect the structure of adult social relationships in nonhuman primates, other important variables being patterns of mating and parenting, and risk of infanticide (e.g., van Schaik and Janson, 2000).

Long-term social bonds between adult males and females are a central feature of gorilla social organization (Watts, 1996). Male silverbacks monopolize most mating activity within their groups and provide protection for females and their offspring. Fe-

males are responsible for staying close to adult males, and spend more time near them than near each other (Watts, 1992, 1994). If social play during development facilitates the formation of social relationships with preferred individuals in adulthood, this explains why female infants prefer to play with males rather than with other females. In particular, it may be argued that by playing with immature males, females begin to adopt the patterns of proximity and affiliation with males that will be characteristic of adulthood. Although young gorilla females are unlikely to maintain the social relationships with their male play partners into adulthood, by playing with males, immature females may learn the characteristics of male behavior in general and acquire flexibility and competence in interactions with males. Similar female preferences for male play partners would also be expected, and in some cases have indeed been observed, in other primate species living in one-male groups or harems, such as hamadryas baboons or gelada baboons (Kummer, 1968; Mori, 1979). In contrast, in less male-centered primate species such as macaques and baboons, immature females typically prefer to play with other females (see introduction for references).

The finding that most social play among gorilla infants occurs with individuals in the same age range (i.e., peers) is consistent with what is reported in other primate species and with the motor-training hypothesis of play, because immatures are expected to play mostly with individuals that are matched for body size and social skills (e.g., Fagen, 1981; Fairbanks, 1993). Mother-infant play is more frequent in the great apes than in monkeys or prosimians (Maestriperi and Call, 1996), but the reason for this difference and the adaptive consequences of maternal play for infant social development are poorly understood. In this study, mother-infant play did not appear to vary in relation to infant sex or age. The observations that male infants tended to play with subadult females more than female infants did, and that only male infants initiated play with adult females other than their mother, are consistent with the social-relationship hypothesis of play, in that immature males should be more interested than immature females in developing relationships with unrelated subadult and adult females. This trend in the partner preferences of male infant gorillas needs to be replicated by future studies with larger sample sizes. Play between infants and the male silverback was infrequent and could not be systematically investigated, in part because one group with 4 infants was without the silverback for most of the study, while another group with the silverback had only 2 infants.

Social play was the most common form of play, and solitary locomotor play the least common. Locomotor play increased in frequency over the first 2 years of life and decreased thereafter. Both object and social play continued to increase in the third year, but decreased in the fourth and fifth year (for

age effects on play in gorillas, see also Schaller, 1963; Fossey, 1979; Hoff et al., 1981; Brown, 1988). Among mammals, locomotor play generally contains elements of antipredator behavior, object play contains elements of predatory behavior and food handling, and social play contains elements of affiliative, agonistic, and sexual behavior (Powell, 2000). The low frequency and early decline of solitary locomotor play in infant gorillas is consistent with the notion that western lowland gorillas are relatively free from predators and exhibit a relatively sedentary lifestyle that is adapted to their ranging and foraging habits (Goldsmith, 1999). The higher frequency of object play, instead, may be instrumental for the development of sophisticated specializations in handling and processing of plants and other food (e.g., Byrne et al., 2001). The overall decline in play in the fourth and fifth year of life is probably associated with changes in time budgets (and in particular an increase in foraging time), as well as with growing interest in other social activities such as agonism and sex (Watts and Pusey, 1993). For example, social play between adolescent and subadult gorilla males ceases altogether as soon as they became sexual rivals (Watts and Pusey, 1993). The developmental time course of different forms of play is therefore the likely result of different processes, including maturation of physical and motor skills, independence from the mother and development of social relationships with other individuals, and allocation of time to different social and nonsocial activities in relation to ecological and reproductive pressures.

In this study, gorilla mothers were never observed to encourage their infants to engage in play or any other social activities with other individuals. Mothers were observed to discourage their infants from playing only on 10 occasions, and without any obvious bias in relation to sex. Maternal discouragement of infant social interaction was more frequent with younger infants than with older infants. These findings are consistent with the view that gorilla mothers with offspring in the 2–4-year age range are generally uninvolved in their social and nonsocial activities, at least within the environmental conditions of this study (Maestriperi et al., 2002). Therefore, there was no hint that the developmental changes in play or the sex differences in play frequency or play-partner preferences observed in this study may have been the result of socialization, and in particular of maternal influence.

Most social play observed in this study consisted of wrestling and chasing. Play faces and mockbites were recorded independently from social play, but the fact that they often occurred multiple times during a bout of play and showed a strong correlation with the frequency of play initiated and received suggests that they may be patterns of play rather than play signals with a communicative function. The mockbite has also been interpreted as a play pattern in gorillas by Schaller (1963) and Dixon

(1981), and the play face could be viewed as an incomplete mockbite (for a noncommunicative interpretation of the play face in primates, see also Pellis and Pellis, 1996). Chest-beating and other displays have been reported to occur during play in both mountain and western lowland gorillas (Schaller, 1963; Dixon, 1981; Brown, 1988; Watts and Pusey, 1993). Since displays become an important component of the agonistic behavioral repertoire of adult males, their use during play, mostly by male infants, is consistent with the motor-training hypothesis of play. Clapping/drumming was exhibited by both sexes and was more specifically associated with the initiation of play. This behavior may serve an attention-getting function, similar to what was reported for chimpanzees (Tomasello et al., 1989). Few or no patterns of sexual behavior occurred during play. This is in contrast with cercopithecine monkeys, in which sexual patterns such as presenting and mounting figure prominently in the play interactions of infants and juveniles (e.g., Chadwick-Jones, 1989). This difference may be explained in part by the fact that presenting and mounting play an important role in the development and maintenance of dominance relationships in some cercopithecines (e.g., Chadwick-Jones, 1989), but not in gorillas.

CONCLUSIONS

The sex differences in social play and play-partner preferences observed among infant western lowland gorillas are consistent with both the motor-training hypothesis and the social-relationship hypothesis of play. Specifically, the higher frequencies of male play and male preferences to play mostly with other males are consistent with the motor-training hypothesis, while female preferences to play mostly with males (and male tendencies to reciprocate these interactions) are consistent with the social-relationship hypothesis. Taken together, the dynamics of play among infant gorillas fit well with the characteristics of adult behavior and social structure in this species. More comparative studies of play and social development in the great apes and other primates are needed to assess the extent to which sex differences in play vary predictably in relation to social structure. In particular, the study of sex differences in play in species with minimal sexual dimorphism or with female dominance (such as bonobos) will be crucial to assess the general validity of the motor-training and the social-relationship hypotheses of play in primates. Although future studies of sex differences in primate play will be crucial to elucidate the functional significance of play in relation to the life histories of the two sexes, a full understanding of play in primates and other animals will also require an appreciation of the interindividual variation and plasticity across development that are characteristic of this phenomenon.

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