

Deception and Evolutionary Biology

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Introduction

Anthropologists have long been interested in questions of human consciousness and perception. It is easy to speculate about the evolutionary origins of such attributes and to construct adaptive scenarios that rationalize the benefits of cognitive capabilities for their possessors in the evolutionary struggle for survival. Too often anthropologists and others interested in the behavioral and neural sciences attributed higher cognitive characteristics to humans without recognizing that other animals may have cognitive capabilities that would seriously question the notion of human uniqueness for conscious thought, self-awareness, and intentional deception. Langer (1972:163) has noted that deception is a distinctly human activity. It seems unlikely, however, that anyone would accept such a clear distinction today, although some anthropologists have expressed doubts about the cognitive capacities of nonhuman species. It is important to note that the similarity in patterns of deceit between human and nonhuman animals has been recognized and clearly articulated for over four decades. Wile (1942:294) states that "there is little difference between the feigning of death by a beetle and the syncope of a man on the battlefield."

In this volume we attempt to view human behavior as a complicated dialogue between biology and culture (see Paul, this volume). It seems to me that deception and its implications for consciousness and self-awareness is one area where the interplay between what we often reserve for humans and a careful scrutiny of the behavior of nonhuman primates may be instructive.

A commonly held view by Rappaport (1979) and others notes that among nonhuman primates deception has only been convincingly demonstrated in apes. "It is not surprising that even for apes for whom lying is evidently possible it is probably uncommon. But for many, if not indeed most other species, lying may not occur because of the stereotyped nature and external control of the specific stimuli" (1979:225). Such reactions to the idea that animals are capable of mentalism (in the psychological sense) go back to C. L. Morgan's (1894:53) injunction: In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of one which stands lower in the psychological scale.

Rarely do anthropologists, biologists, and psychologists focus on the same issue and come to any consensus on the essential aspects of a problem. The challenge of this article is to bring together lines of evidence from a variety of sources that shed light on a pattern of behavior that some have maintained is a nearly exclusively human behavioral characteristic, namely deception. This article reviews some general characteristics of deception, some variables that influence its expression, some particularly instructive examples of deception in three nonhuman primate species, and some possible behavioral arenas where deception might have gained an evolutionary toehold. One of the first issues that must be raised is: Why invest time and energy in the study of deception? Why is deception a significant behavioral pattern that demands careful investigation? It seems that deception is a subset of behaviors that evolutionary biologists have come to view as strategizing behaviors. These strategizing behaviors all center around the theme of fitness maximization and reflect an emerging view by many scientists that for a complete understanding behavior must be explained at multiple levels, not the least of which is at the level of ultimate causation (Tinbergen 1963). In this view we can see the activities of animals as elements of a behavioral program whose goal is the maximization of inclusive fitness (Daly and Wilson 1983). This article does not suggest that all human or animal behavior is strictly fitness maximizing, but it will work from the rapidly accumulating body of data, the preponderance of which suggests that much of behavior can be profitably viewed in this manner. See Boyd and Richerson (1985:12-13, also chapter 5) for an important discussion of the critical assumptions of sociobiology, particularly when applied to humans. I am chiefly concerned with the observation that nonhuman primates practice deception, since some (Marshall 1970) have noted that such behavior constitutes compelling evidence of consciousness and intention in nonhuman animals (see Boyd and Richerson, this volume).

One important point that I will return to later is the precise specification of the social as well as the ecological conditions under which deception may occur. The study of deception is also important because it is necessary to understand the various contexts that may set the stage for the selection of alternative forms of "honest" behaviors. Phrased differently, how do alternative and necessarily rare forms of behavioral patterns emerge in an evolutionary perspective? As I hope to demonstrate, for deception to be successful it must be an infrequent occurrence.

I do not intend to propose a new definition for deception but simply to borrow from the work of several others some important characteristics of deceptive acts that might be useful for purposes of identification. First, it is important to distinguish between intra- and interspecific deception. Examples of interspecific deception abound in the literature and can be generally characterized in terms of predator-prey relations. Predator and prey are often concealed from each other, and this has led to amazing examples of camouflage and mimicry. In the instances of camouflage, an individual attempts to remain invisible against the background, while in instances of mimicry the organism seeks to resemble something specific; it may be cryptic, but it is often conspicuous. Deceit in communication need not only involve exaggeration of one's capabilities, but in the more general case it can

lead the receiving individual to an inaccurate assessment of the environment. Deceit should theoretically be favored when the sender is able to cause the receiver to err in assessing its surroundings, since this would likely reduce the fitness of the receiver and increase the fitness of the sender. In this respect it is likely that deceit is more common between species than within species. Nonetheless, for my purposes I wish to focus on the comparatively rarer type of intraspecific deception, for that is where I believe we potentially gain some insight into the evolution of conscious thought and self-awareness.

In recent work on deception in nonhuman primates, Byrne and Whiten (1985) note a number of characteristics of deception. First, deceptive acts must be low-frequency events that are part of the natural repertoire of the species. For deceptive acts to be successful they must be relatively rare events and they must be undetectable, at least some of the time by the recipient. It is important to note that familiarity between individuals may be an important aspect of deceptive behavior in nonhuman primates. Unlike scorpion flies (Thornhill 1979) where any given male is not very likely to encounter the same female twice, nonhuman primates generally live in stable groups whose composition changes little over time. Individuals are known to one another and therefore to be successful, deceptive acts must be rare frequency-dependent events.

Whiten and Byrne (1986) also recognize the difficulties associated with deception in small close-knit groups of primates. They note that tactical deception in such intimate circumstances may be underreported in the animal behavior literature, because the behavior is likely to be subtle and relatively rare events. Moreover, the data on deception are likely to be anecdotal, and researchers are conservative about reporting it. Whiten and Byrne (1986:672) define intimate-tactical deception as (1) acts from the normal repertoire of the individual (2) used at low frequency, and in contexts different from those in which it uses the high frequency (honest) version of the act (3) such that another, familiar individual (4) is likely to misinterpret what the acts signify (5) to the advantage of the actor. Finally, to be evolutionary successful, a deceptive act must confer a benefit to the perpetrator, or at least impose a cost to the target of the act that enhances the fitness of the perpetrator relative to other competing individuals.

While not the primary focus of this article, I think that it is important to make a few remarks about causality and deception. It is tempting to engage in armchair theorizing about the proximate mechanisms involved in deception. All too often, individuals ask what evidence exists that animals are aware of what they are doing, presumably exercising some conscious control over their behavior as opposed to acting out some rigidly encoded behavioral program. In my opinion, this dichotomy is a false one, and deceptive acts should be viewed only in terms of the outcome. As Donald Griffin (1984) puts it in his book *Animal Thinking*, some innately coded behavior in ourselves may be accompanied by awareness, such as sneezing or having a baby. On the other hand, some learned behaviors can drop out of the realm of consciousness unless particularly challenging circumstances occur. For example, much of driving a car is unconscious, particularly if there is someone else to talk to, and only becomes conscious when some decision must be

made. While we have not reached a point where the complex interconnections between biology and behavior can be spelled out with precision, the nature of these interconnections is an empirical question open for study by scientists from a variety of different perspectives.

It occurs to me that the most difficult problem, and one that causes the most concern on the part of most scientists who consider this problem of deception, is the notion of intentionality. Inevitably one must ask what evidence is there that the animals were aware of what they were doing as opposed to acting out some genetically encoded behavioral program. There are at least two ways in which one might be reasonably confident that the observations labeled *deception* included some awareness on the part of the animal. First, it is important to note the intra- and interanimal variation in behavior. If an animal engages in the same behavior pattern under what appears to be the same set of conditions in repeated rigid fashion, we would be inclined to call such behavior genetically encoded. On the other hand, if there were sufficient variation in response and flexibility of behavior patterns within and between individuals under what appears to the same set of environmental conditions, one would be tempted to label such behavior as learned, or at least not coming under tight genetic control. It could be argued that what animals are learning is to differentiate between successively finer and finer stimuli and make increasingly more subtle responses. I do not wish to engage in an argument concerning learned vs. genetically programmed behavior, for I assume that there is a complex interconnection between these aspects of behavior.

One of the most important tasks in understanding the expression of deceptive behavior is the enumeration of the variables that may influence its expression and frequency of occurrence. I will consider four variables that may influence the expression of behavioral deception: (1) the relative cost/benefit analysis, (2) the ontogenetic development of the individual, (3) the ecological constraints of the habitat, and (4) the general pattern of social organization. One of the critical determining variables for the expression of deception is the relative cost/benefit ratio to individuals engaged in an interaction where a potentially deceptive act can occur. Dawkins and Krebs (1978) have noted that there may be unequal costs and benefits to individuals engaged in a contest. Imagine that two individuals are competing for the same food item, and they are identical in every characteristic, except one had recently eaten and the other is hungry. One would predict that the hungry individual would win. A male grasshopper calling to its mate has a great deal more at stake than a monkey squabbling over a morsel of food (Krebs and Dawkins 1984). Consider when a fox chases a rabbit, the rabbit is likely to win in most cases because the fox is merely running for its dinner, while the rabbit is running for its life (Dawkins and Krebs 1979). It makes sense then that deception and detection of deception may very well have different costs and benefits for the interactants and therefore be subjected to very different selection pressures. As Dawkins and Krebs (1978) note, probing and assessment may limit the extent of interspecific deception, but the lack of intraspecific deception still requires an explanation. Successful deceit requires two things: (1) that the deceit must be relatively rare, and (2) that the responder must be unable to detect the deception at

some times. Wallace (1973) further notes that intraspecific deception is limited by the fact that the deceiver and responder are members of the same gene pool.

Another variable that may affect the expression of deception is the basic ontogenetic pattern of development of the species. Just as Marler (1985) has summarized much of the recent work on vervet monkeys (*Cercopithecus aethiops*), showing that they improve in their ability to discriminate among various types of predators with increasing age and thus make fewer inappropriate responses to nonthreatening species, individuals are likely to improve in their ability to deceive as well as detect deception. Ontogeny surely must play a role in the development of both the physical as well as the social skills necessary for successful deception. Moreover, as there are ontogenetic differences within species, there are clear differences in ontogeny across species that likely affect the potential expression of deception.

In a larger sense, one must not fail to recognize ecological factors will likely place constraints on the expression of deception. Conditions of captivity may enhance or reduce the probability of deception, depending on such things as social conditions, group size, cage size, or opportunities to be out of visual access of all group members. In the free-ranging situation it seems likely that the distribution of critical resources, whether they be food items, sleeping sites, or sexual partners, will influence the expression of deception and its success relative to "honest" variants of the particular behavior. In socially living primates where there is unequal distribution of critical resources among group members (including, but not limited to, a knowledge about the social and physical environment) we may see the evolution of deceptive behavior. Clearly, a species may respond with an increased frequency of deceptive behaviors if information about more than one of these critical resources is unevenly distributed among group members.

Species-typical patterns of social organization may influence the incidence of deception. A species that forms large groups and is spread over a wide area while foraging may be more generally predisposed toward deception than a species who tends toward small group size, restricted home range, and highly coordinated feeding activities. In this case, the general prediction would be that chimpanzees would be more likely to practice deception than gibbons. Unlike gibbons, who tend to live in monogamous pairs in a well-defined territory, chimpanzees exhibit a much more fluid pattern of social organization with individuals as well as subgroups moving independently of a larger social group.

No doubt there are a number of other variables that affect the expression of deception, but one problem that plagues the study of deception is, paradoxically, one of its defining characteristics, namely its low frequency of occurrence. Discussions of deception have centered largely on anecdotal accounts of behavior that were interpreted as deceptive. Quiatt (1984:26) cautions, "Most reports of deception by monkeys and apes in natural circumstances necessarily involve isolated incidents, and one cannot but distrust anecdotal accounts in which the assessment of intention is dependent upon an observer's ability to retrospectively distinguish clearly between at least three possibilities: a) intentional deception by the communicator; b) misunderstanding of goals by the signal-recipient (no de-

vious intent or deception assumed); and c) correct statement but subsequent substitution of goals by the communicator (again no devious intent or deception assumed)." Quiatt notes further that sampling problems underlie the frequency of anecdotal accounts of deception in the natural setting. Clearly such anecdotal data will likely never be amenable to precise quantitative analysis, but is that an a priori reason to abandon such data collection? I think not! It seems to me that researchers should be able to develop an objective set of criteria that would allow a more precise categorization of deceptive behaviors, that would render cross-species comparisons not only possible, but extremely important. Moreover, such objective criteria should avoid the use of anthropomorphic description and instead allow the careful description of the acts themselves to dictate the classificatory scheme.

Classification of different types of deception hinges on the extent to which they require volitional control of behavior. By this I mean the extent to which the individual organism has control over the choice of behavioral options. Certainly, we can explain a considerable amount of deception in simple stimulus response terms. Classic examples of mimicry can be explained in Morgan's terms most parsimoniously as the discrimination of complex stimuli by an organism. In order to determine the extent of volitional control of behavior one must observe the organism over time in relatively the same set of conditions, as well as other members of the species under similar as well as different conditions. Only when the degree of variation in response is well documented can we begin to understand the nature of the deception. If there is variability in response within and across individuals, we can speculate that there is some level of individual control of behavior and hence the possibility of intentional deception.

Selected Examples

Whiten and Byrne (1986) as well as Mitchell (1986) have collected an impressive array of examples of deceptive acts among many various species. While I will not review their work here, I will relate three examples of deceptive acts that illustrate the complexity of the behavior patterns involved. Moreover, I would also suggest that while we see deception occurring in a variety of nonhuman primate species, apes and especially chimpanzees (*Pan*) regularly engage in complicated acts of deception.

While I have outlined some variables that affect the expression of deception, it is clearly manifest in competition over food and mates. Kummer (1982) reports an interesting observation of deception in hamadryas baboons (*Papio hamadryas*). A juvenile female hamadryas baboon in estrus leaves her adult male leader and repeatedly mates with a juvenile male behind a rock where the leader cannot see her. Between matings, she goes to where she can peek at the leader, or even approaches him and presents herself to him before she again mates with the juvenile in the hiding place. "A female spent 20 minutes edging herself into a sitting position where a rock hid her front and arms from her leader while allowing him to see the top of her head and her back. She thus groomed a subadult male, an

activity which is not often tolerated by leaders. The leader was able to see that she was present, but not what she was doing'' (Kummer 1982:118-119).

Strum (cited in Jolly 1985:412-413) notes that savanna baboons (*Papio anubis*) are capable of clever deceptive tactics. One of the female baboons at Gilgil grew particularly fond of meat, although males do most of the hunting. A male, one who was not willing to share, caught an antelope. The female edged up to him and groomed until he lolled back under her attentions. She then snatched the antelope carcass and ran. On another occasion the same male had meat and the female again groomed him. He kept his hand on the meat. She stopped grooming him and began chasing his favorite female. He then went to his friend's aid, abandoning the carcass. The original female then returned to the carcass and snatched the antelope.

Among chimpanzees (*Pan troglodytes*) mutual bluffing displays are fairly common and relate to unsettled dominance relationships. In a complicated but fascinating example of deception, de Waal (1982, 1986) notes that during bluffing displays males may show a combination of fear and aggression. Fear is manifest by teeth-baring, but is not shown in the presence of the rival male. Typically, the bluff displays are resumed only after the disappearance of the fear facial expression. De Waal (1982:133) observed the following: "The two males Luit and Nikkie did their best to show not the slightest trace of uncertainty in each other's presence . . . During one of their confrontations . . . after they had displayed for over ten minutes a conflict broke out between them in which Luit was supported by Mama and Puist. Nikkie was driven into a tree and began to hoot at the leader again while he was still perched in the tree. Luit was sitting at the bottom of the tree with his back to the challenger. When he heard the renewed sounds of provocation he bared his teeth and immediately put his hand to his mouth and pressed his lips together . . . I saw the nervous grin appear on his face again and once more he used his fingers to press his lips together. The third time Luit finally succeeded in wiping the fear grin off his face only then did he turn around. A little later he displayed at Nikkie as if nothing had happened and with Mama's help he chased him back into the tree. Nikkie watched his opponents walk away. All of a sudden he turned his back and began to yelp very softly. I could hear Nikkie because I was not very far away, but the sound was so suppressed that Luit probably did not notice that his opponent was also having trouble concealing his emotions."

Byrne and Whiten (1985:670) observed another interesting example of deception over food in chacma baboons (*Papio ursinus*). A juvenile used screaming, normally associated with attack or threat by another individual, to gain access to underground food items that normally require extensive digging or loosening of turf from hard soil. Adult females were deceived by juveniles into abandoning the area they were excavating for deep growing corms because they were alerted by the juveniles that a threat or attack was imminent. Immediately after abandoning the area the juvenile obtained the food. A similar observation was made by Byrne and Whiten (1985:671) concerning an adult male baboon. The previous alpha male of the group was in the process of being deposed by a younger male. The

senior male was displaced from a rich source of underground food items in loose turf by the younger male. The deposed leader moved away briskly. Within three minutes all six individuals that were feeding at the patch moved off following the deposed senior male including the younger usurper. All six were duped, however, for within two minutes the senior male returned to the feeding patch to feed by himself.

Goodall (1971:96–97) observed the following: Figan, cleverest of the Gombe chimps, learned as an adolescent that he could lead males away from the banana pile by striding confidently into the woods. He then returned, by another route, to feed unmolested. On one occasion he “spotted a banana in a tree that the older chimps had overlooked, but Goliath was resting directly underneath it. After no more than a quick glance from the fruit to Goliath, Figan moved away and sat on the other side of the tent so that he could no longer see the fruit. Fifteen minutes later, when Goliath got up and left, Figan, without a moment’s hesitation, got up and collected the banana.” He had apparently sized up the situation and realized that he could not snatch the banana with Goliath there and that he could not help looking at the banana which would guide Goliath’s own gaze to the prize. This pattern of leaving and then surreptitiously returning developed as a strategy for Figan. Once, however, Goodall (1971:97) reports that Figan’s clever tactics did not work. He led a group of chimps into the woods only to return to the banana box and find another high ranking male in his place. “Figan stared at him for a few moments and then flew into a tantrum, screaming and hitting at the ground.”

De Waal (1982:73) provides yet another example of the behavioral flexibility and intelligence of chimpanzees. “Dandy (in the throes of puberty) has to offset his lack of strength by guile. I witnessed an amazing instance of this together with German cameraman Peter Fera. We had hidden some grapefruit in the chimpanzees’ enclosure. The fruit had been buried in the sand, with small yellow patches left uncovered. The chimpanzees knew what we were doing, because they had seen us go outside carrying a full box of fruit and they had seen us return with an empty box. The moment they saw the box was empty they began hooting excitedly. As soon as they were allowed outside they began searching madly but without success. A number of apes passed the place where the grapefruit were hidden without noticing anything—at least that is what we thought. Dandy too had passed over the hiding place without stopping or slowing down at all and without showing any undue interest. That afternoon, however, some three hours later when all the apes were lying down dozing in the sun, Dandy stood up and made a bee-line for the spot. Without hesitation he dug up the grapefruit and devoured them at his leisure. If Dandy had not kept the location of the hiding place a secret, he would probably have lost the grapefruit to the others. . . . Dandy’s resolute return to the hiding place took us so completely by surprise that Peter Fera was unable to film the incident.” De Waal (1986:228) notes that the size of the enclosure and his controlled and deliberate manners exclude the possibility of his accidentally finding the fruits.

In another example of behavioral camouflage, de Waal (1986:228) reports that an adolescent female chimpanzee observed a zoo visitor throw a small apple

into the enclosure. Instead of rushing to the spot and picking it up, she moved quietly toward the food and sat a few meters from it. After several glances she moved closer to the fruit and placed her hand near it, and without looking down grasped the apple in her hand. She then walked away normally, an unusual posture since chimpanzees usually walk on three legs while carrying food. Then at a quiet place out of visual access to the other group members she sat and ate the apple.

Chimpanzees have long been known for their intellectual abilities, and the capacity for deception has been demonstrated in both the laboratory and field conditions. In one of the most often cited studies of chimpanzee communication, Emil W. Menzel made a fascinating observation on the behavior of a small group of chimps housed in an outdoor enclosure at the Delta Primate Research Center. Probably the clearest evidence that the chimpanzees knew what effect their behavior was having on others occurred in some interactions between Rock (the most dominant chimp as well as a relative stranger) and Belle (long-term resident) over a period of several months. When tested when Rock was not present, Belle invariably led the group to food and nearly everybody got some. In tests conducted when Rock was present, however, Belle became increasingly slower in her approach to the food. The reason was not hard to detect. As soon as Belle uncovered the food, Rock raced over, kicked or bit her, and took it all. Belle accordingly stopped uncovering food if Rock was close. She sat on it until Rock left. Rock, however, soon learned this, and when she sat in one place for more than a few seconds, he came over, shoved her aside, searched her sitting place, and got the food. . . . Eventually Belle sat farther and farther away, waiting until Rock looked in the opposite direction before she moved toward the food at all—and Rock in turn seemed to look away until Belle started to move somewhere. On some occasions Rock started to wander off, only to wheel around suddenly precisely as Belle was about to uncover the food. Often Rock found carefully hidden food that was 30 feet or more from Belle, and he repeatedly oriented at Belle and adjusted his place of search appropriately if she showed any signs of moving or orienting in a given direction. If Rock got very close to the food, Belle invariably gave the game away by a “nervous” increase in movement. However, on a few trials she actually started off a trial by leading the group in the wrong direction, and then, while Rock was engaged in the search, she doubled back rapidly and got some food (Menzel 1974:134–135; 1984).

De Waal notes that falsification is the most elaborate type of deception practiced by chimpanzees at the Arnhem Zoo. He describes an interaction between two chimpanzees, Nikkie and Spin, that has the appearance of purposefulness and forethought (1986:235). During charging displays, Nikkie often carries a weapon in his hand, often holding it behind his back (de Waal 1982:82). Nikkie aggressively pursued a female, Spin, who sought cover behind a tree trunk. Nikkie started to turn to the left and Spin responded by moving to the right. At the moment Spin appeared from behind the tree trunk Nikkie threw a brick, but almost without losing speed, so that he was able to catch his victim when she jumped back to the left in order to avoid the projectile. This observation, de Waal argues,

should be classified as intentional deception as it deceptively created a false opportunity to escape on the part of the victim. The speed and fluidity of the action do not lend themselves to a stimulus-response explanation.

Because of their low frequency, the scientific study of deceptive acts must rely on long-term studies of known populations of individuals. The recognition of deception is in no small part dependent on an intimate familiarity with the behavioral repertoire of the species. Such a familiarity will allow precise differentiation between honest and deceptive variants of a behavioral pattern. Convincing demonstrations of deception in its evolutionary context should come from the laboratory as well as field studies. As previously noted, however, certain ecological and social conditions may increase or decrease the frequency of the behavior.

If it is unlikely that any funding agency is going to support a prospective study of deception, then how do we proceed? It seems to me that behavioral researchers need to be alerted to the possibility of the occurrence of deceptive acts, and adequate criteria for their identification should be widely disseminated. Moreover, those researchers engaged in both field and laboratory studies where the general ecological and social conditions likely to promote the expression of deception are found, should be particularly attuned to the recording of deceptive encounters.

Evolutionary Considerations

Robert Trivers (1985) has noted that systems of animal communication have *not* necessarily evolved for the dissemination of the truth. Systems have evolved for transmitting information, misinformation, or both. It is likely the case that deception is a parasitism of the preexisting system for correct communication. Whatever the case, there exists a coevolutionary struggle between the deceiver and the deceived. There is an evolutionary arms race to develop better deception tactics and subsequently the pressure to develop better deception detection devices. Better deception detection devices can take the form of a devaluation of the association of the signal and response or involve the use of supplementary signals for finer discrimination. Moreover, the struggle is frequency-dependent. That is, as deception increases in frequency, it intensifies the selection for detection, and as detection spreads, it intensifies the selection for deceit. Van Rhijn and Vodegel (1980:641) note that if individual recognition in small groups of animals has been an important evolutionary consideration, then cheaters can hardly evolve because they will be recognized.

Interestingly, as the powers to deceive and the powers to detect deception are being improved by natural selection, a new kind of deception may arise: self-deception. Self-deception renders the deception unconscious to the deceiver and therefore makes the deception all the more believable because subtle signs of self-knowledge are not apparent. This subtle form of deception makes its most dramatic appearance in human language. As my colleague Melvin Konner noted in his book *The Tangled Wing: Biological Constraints on the Human Spirit*: "Language may have as one of its major functions deception—the covering of base emotions or the distortion of them to make them look pure" (Konner 1982:169).

It may be argued that there are at least three areas in the logic of evolutionary biology of behavior that provide a theoretical starting point for the evolution of deception. These areas are adult mating strategies, parent/offspring conflict, and social play between unequals or asymmetric partners. From the abundant examples of clandestine sexual activities in both Old World monkeys and apes, the withholding of information about sexual activities from other group members must have played a role in the evolution of deception. This clandestine mating pattern might easily have been of importance where dominant animals engage in a significant proportion of the total mating opportunities, and only through deceptive behavior can less dominant individuals secure any mating opportunities. See the previous example of the young female hamadryas baboon and her efforts to remain partially hidden from her harem leader while grooming a younger and less dominant male (Kummer 1982).

Fagen (1981) has developed a model that suggests that deception could evolve in situations where two sibs are playing and there are two strategies that any individual can employ. In Fagen's formulation, the two sibs differ in their optimum level of play. In his model he argues that deception or misinformation could evolve when each sib tries to exaggerate its own benefit while deemphasizing the other's benefit in order to give the situation the appearance of one in which both would agree on the style of play. The misinformation could be communicated by exaggerated displays of enjoyment (laughter, antics, etc.) during one partner's style of play, and by exaggerated protests (pain vocalizations, struggling, threatening, etc.) during the preferred partner's style of play (Fagen 1981:426). It may also be that deception itself is practiced during play (Thorpe 1972). Therefore, one can at least argue that in the play of young animals we find a behavioral arena that could serve as an evolutionary proving ground for deception.

Another area in which the evolution of deception could be envisioned is the context of parent/offspring conflict (Trivers 1974). In this situation, parents and offspring disagree over the termination and amount of parental investment. Children ought to have evolved sophisticated techniques to induce more parental investment than would be in the best interests of the parents. Conversely, a parent will minimize resistance in its offspring if it can convince the offspring that it is acting in the offspring's best interest, when it is merely expressing its own self-interests. Deception in this context seems to have a natural ally in parental domination (Trivers 1985). Keep in mind that offspring do not take this lying down, and if they are at a disadvantage they should employ psychological tactics to induce more parental investment. Temper tantrums and regressive behavior by youngsters are examples of such potentially deceptive strategies; temper tantrums because of the threat of self-injury, and regressive behavior to induce more parental investment by reverting back behaviorally to a period when parental investment was easier to obtain. From these examples it can be seen that wherever there exists disparity in intrinsic competitive abilities or knowledge, we find a unifying condition for the evolution of deception.

Experimental Evidence

Finally, it is important to review the available data to determine if there are any critical experiments that would inform these anecdotal observations of deception. Woodruff and Premack (1979) developed an intriguing laboratory experiment using four chimpanzees that addresses the central question of this section, the development of deception. In their study of communication between chimpanzee and humans in which each member of the dyad served alternately as sender and receiver of information, they found the following: Initially the animals behaved the same way in the presence of both the cooperative and competitive trainers, and consequently without regard for whether or not it gained them access to food, but changes in their performance over the course of the experiment suggest the development of intentional communication. When serving as recipients, three of the four subjects ultimately learned to controvert the competitive trainer's cues by avoiding the location to which he oriented. When serving as senders, their behavior patterns soon changed form: some responses which provided little information (e.g., changes in rocking motions) disappeared, while more explicit cues either increased in frequency (e.g., glancing at a container, approach) or appeared *de novo*, and in one case the latter outcome happened quite suddenly (pointing for Jessie). The chimpanzee's behavior changed over time and became more deliberately informative. Early in the experiment chimpanzees roamed about the test enclosure and only occasionally glanced at the food containers, requiring caretakers to make their choices by observing which side of the enclosure the animals spent more time in. By the end of the experiment, the animals quickly oriented toward the food, and glanced repeatedly back and forth from the food container to the caretaker. More revealing was the development of a difference in the amount of information conveyed to the two trainers. All subjects learned to convey or withhold information, depending on whether their goal in obtaining the food for themselves was in agreement (cooperation) or at odds (competition) with that of the trainer. Thus the chimpanzees demonstrated an ability to take into account the nature of the recipient in choosing whether or not to impart information. Finally, two subjects consistently misinformed the competitive trainer, and these instances of deceit meet the most stringent behavioral criteria for intentional communication (Woodruff and Premack 1979:355-356).

One question about Woodruff and Premack's evidence is to what extent did the subject want the trainer to believe the food was in a particular container? Further information could be gained by experimental probing of the transmission of misinformation between subject and trainer. A crucial experiment would be to place the food in plastic, see-through containers and instruct the bad trainer to look at these containers upon entering the room. If the chimpanzee instantly recognizes a logical inconsistency between what it wants the trainer to believe and what the trainer obviously knows, then we would have evidence for conscious deceit (Seyfarth et al. 1982:397). See Dennett (1983:349) for a refinement of the basic test. Although as Menzel (1983:371) notes, his previous work (Menzel 1971, 1974; Menzel and Johnson 1976, 1978) precedes these discussions and tests of deception and cognition.

Concluding Remarks

“If deception and lying are so widespread in the animal and plant kingdom and if this behavior seems to serve an important survival function, we at least might question whether some similar mechanisms govern the behavior of humans in their social encounters” (Ludwig 1965:15). From this review it is clear that animals and particularly nonhuman primates use a variety of strategies, some of which involve components that appear to humans to be deception in the conventional sense of the word. What I have tried to do is to place the examples of deception into a coherent framework, which does not spell out in great detail, but in large brush strokes, how such behaviors might have evolved. Clearly, when we carefully examine the behavior of nonhuman primates and in particular, the Great Apes, we find abundant examples of behavior that is so complex that it serves as a useful analogue for much human behavior. Moreover, the study of deception in nonhuman primates provides a context and perspective for the human capacity for deceptive behavior.

Notes

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