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43 Darwin's Continuum and the Building Blocks of Deception

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Deception in nonhuman animals is one of the most fertile areas of research for pursuing philosophical questions in cognitive ethology, but it is an area rife with controversy (Byrne and Whiten 1988; Whiten and Byrne 1988.) The literature on deception is interwoven with questions and claims about intelligence, levels of representation, intentionality, and consciousness (Dennett 1983; Mitchell 1986; Perner 1991). Our aim in this essay is not to survey or evaluate the entire literature; rather, we use the phenomenon of deception as a case study, in a framework of some relevant conceptual distinctions, to illustrate a point about the graded continuity of mental phenomena across species.

Darwin stated: "If no organic being excepting man had possessed any mental power, or if his powers had been of a wholly different nature from those of the lower animals, then we should never have been able to convince ourselves that our high faculties had been gradually developed. But it can be shewn that there is no fundamental difference of this kind" (Darwin 1871/1936, p. 445). That is, while there may be notable differences among closely related living species because of rapid evolutionary changes and lost ancestral varieties, given the theory of natural selection, there should be no inexplicable jumps in cognitive abilities. Conversely, when faced with what seem to be differences *in kind* between related species' abilities, we should look for other cognitive abilities that may underlie these differences (cf. Allen and Bekoff 1997; Pinker 1994 and Deacon 1997 discuss language in this context from different perspectives).

With this in mind, we examine the traditional distinctions between levels of deception in animals and suggest some cognitive abilities that may serve as building blocks to account for the apparent gaps between these levels, focusing on the order of primates. We then describe an experiment that tested for deception in lemurs and that suggests directions for further empirical work in this area.

Three Categories of Deception

Deception may be broadly defined as an agent's producing or withholding an act or a signal so that it is misinterpreted by another to the advantage of the agent (see Mitchell 1986 and Hauser 1996; cf. Whiten and Byrne 1988; Hauser 1997). As such, deception always involves misrepresentation, and it takes (at least) two animals to make misrepresentation lead to deception. These animals may be of different species (e.g., predators and prey) or the same species, as in the case of "sexual mimicry" (Wickler 1965, 1968; see also Hockham 2000, 2001; and Weldon and Burghardt 2001, for a discussion of the link between mimicry and deception) or in instances where one monkey leads another way from a known food source (see later discussion).

However, if we are interested in determining what sorts of cognitive abilities are needed to carry out different types of deception, we should not begin by looking at the complexity of the misrepresentation. Sometimes the use of fairly simple signals to deceive (e.g., a misdirecting eye gaze) may require significant cognitive abilities, whereas there may be no cognition at all behind informationally rich displays of misrepresentation (e.g., butterfly wings with intricate patterns that make the wing ends look like the butterfly's head) (Robbins 1981). Camouflage and other "hardwired" displays count as deception in our broad first-pass definition, as long as we allow the production of signals to include the production (or even possession) of misleading appearances.

In our view, the relevant gradations in the cognitive abilities involved in deceptive signals or behaviors should be delineated by the historical processes that produced them, the flexibility

with which they can be displayed, and the degree to which the deceiving animal understands how the deception achieves a desired outcome. Many discussions of animal deception suggest these distinctions by classifying deceptive behaviors in three basic categories, which are distinguished along the same lines as many other apparently intelligent behaviors: genetic, learned, or intentional (Mitchell 1986).

In the first category, there are the apparently "hardwired" deceptive behaviors, such as the Mantis shrimp that "pretends" it is ready to fight a competitor even though its shell is soft from molting (Caldwell 1986) or the nonpoisonous butterfly that mimics the coloration of poisonous butterflies to ward off blue jays, a common predator (Brower 1969). In both of these cases, the misrepresenting organism does not *choose* to misrepresent, with the intention to deceive, among other possible behaviors. In fact, what it does is simply what it cannot help doing. The behaviors or traits do not get acquired through experience or modified through a history of learning. Rather, they are produced by a history of selection for certain genetic "programs." As such, they are relatively inflexible in the face of environmental contingencies (although they may require environmental cues to develop). This type of deception roughly corresponds to what Dennett (1983) characterizes as "zero-order intentionality," since the animal does not seem to represent the goal of its deceptive behavior (the behavior does not involve beliefs and desires).

There is, nonetheless, a difference between these two cases. In the case of the butterfly, the misrepresenting appearance is displayed in individual butterflies whether or not blue jays are around (although the existence of predators provided the selective pressures for the evolution of the wing display). On the other hand, the misrepresenting display of the molting shrimp (the extension of its claws despite its inability to use them), even if it is also the result of selective pressures, is brought forth neither randomly nor all the time, but only on occasion—when there is

a threatening intraspecific competitor, and only one of a certain size (Steger and Caldwell 1983; Caldwell 1986). In this sense, the shrimp requires more resources to be a deceiver than the butterfly. The butterfly just needs to "be," whereas the shrimp needs a perceptual system to detect the appropriate stimuli so that its misrepresentational system can be triggered. Even though the shrimp does not *decide* to display its claw any more than the butterfly decides to maintain its wings' visual appearance, the shrimp has the elemental ingredients that are necessary for the learning involved in the next level of deception; for instance, a perceptual system and mechanisms to discriminate among various situations. As such, the butterfly and the Mantis shrimp occupy neighboring but nonetheless different gradations in Darwin's continuum (see Mitchell's 1986 distinction between levels I and II).

The second category of deceptive behavior is typically described as involving (merely) behavioristic learning. An animal's normal behavior is transferred to a different context because it is reinforced by the rewarding reactions of a target animal when the target animal responds to the behavior as if it indicated something that it does not. Put more simply, the deceptive animal learns to do something because it pays off, and it pays off because the target animal misrepresents the behavior (but the deceiver need not connect the payoff and the misrepresentation; that is, it need not recognize *why* its behavior is effective). For instance, a young monkey is threatened and calls out for help, and his mother comforts him by allowing him to suckle. He learns to associate calling out with getting milk, so when he is hungry, he calls out as if he is threatened. The behavior is deemed deceptive in that the mother reacts as if the call indicates a threat even when it does not.

Such learned behaviors, although they may be relatively inflexible once learned, are not produced directly by a history of natural selection, but rather by particular environmental contingencies, by a history of reinforcement. This type

of deception is similar to Dennett's (1983) concept of "first-order intentionality," because the animal does represent the goal of its deceptive behavior described from the "intentional stance."

Notice that for both genetic and learned cases of deception, the deceiver does not intend its behavior (or signal) to be deceptive. Indeed, its behavior is deceptive only in the sense that we (human observers) describe it that way, and we describe it that way only because the behavior causes the target animal to represent its environment in a way that we know is mistaken. Both the deceiver and the deceived are just going about their business, reacting to perceptual information in the only way they know how. We might say that the deceiving animal produces deceptive behaviors just because the behaviors *have* worked (in its phylogenetic or ontogenetic history), rather than because the animal understands how they *will* work; that is, by causing the target to misrepresent its environment.

The third category of deceptive behavior is thus portrayed as the only one that really fits our ordinary concept of human deception. This category involves deception that can be described as intentional in the sense that the deceiver *intends* to misrepresent information to its target in order to achieve some kind of goal. The crucial point is that the animal understands *how* its behavior deceives its target; that is, the deceiver recognizes the relationship between the target's mental states (e.g., perceptions, beliefs, desires) and its behavior, and the deceiver manipulates those mental states accordingly. Because it involves misrepresenting information so that the target behaves in a particular manner, such deception is sometimes labeled as "reasoned" or "planned."

This third category of deception corresponds approximately to Dennett's (1983) notion of "second-order intentionality" because the deceiving agent represents the beliefs, desires, and intentions of the target, although it may involve higher levels of intentionality as well. For instance, a clever child who wants her pesky brother to leave her room tells him that it's time for his favorite television cartoon. She knows that because he desires to watch the show, then if he believes it is on, he will leave to watch it, satisfying her goal. She creates a false belief in her brother that combines with desires she knows he possesses in order to make him act in a way that he would not have acted without the false belief. Note that one may create a false belief in another's mind with only a limited understanding of the nature of belief. For instance, children pass false-belief tasks and begin intentionally deceiving around age 4, without yet being able to conceptualize and articulate how they are doing so (e.g., Perner 1991, chapter 8; cf. Flavell 1999, 2000).

Building Blocks of Deception

It is notoriously difficult to distinguish between these three categories of behavior—genetic, learned, and intentional—whether dealing with deceptive or other intelligent behaviors. This is in part because, experimentally, the evidence is difficult to gather and in part conceptually because they exist along a continuum without such clear, simplistic dividing lines. We have already suggested a possible building block—perceptual and discriminatory mechanisms—that may underlie the transition from genetic to learned deception. The transition from learned deception to intentional deception may have even more gradations. In fact, it is unlikely that any nonhumans, even the great apes, have a well-developed understanding of how intentional deception works, at least according to most definitions of intentional deception. The reason is quite straightforward. These definitions generally hold that intentional deception requires a theory of mind, the ability to understand that others have beliefs and desires, and there is little persuasive evidence that any nonhuman animals are capable of this (Perner 1991; Whiten 1997). Full-fledged intentional deception may even require language (notice how difficult it is to come up with examples of inten-

tional deception that do not include language—we usually create false beliefs by *telling* lies).

Thus we believe future research should be directed toward identifying the kinds of deception that are intermediate between learned and intentional deception and specifying the cognitive abilities that could underlie such deception. Perhaps the first step in this endeavor is acknowledging that an animal may misdirect another's behavior and understand how it is achieving this goal without necessarily understanding the mental states of its target as mental states; that is, without having a theory of mind.

In fact, we think that it is crucial to delineate this capacity, and propose to call it "proto-understanding of agency," an ability that is more sophisticated than the mere perceptual identification of different elements in one's environment (food, mate, predator, etc.) but more elementary than the recognition of mental states in others. What is sufficient for the presence of proto-understanding of agency is some ability (which itself can occur in gradations) to recognize that certain things in one's environment, such as conspecifics, prey, or predators, can be manipulated in very specific ways—ways that do not apply to various other things, including many other animals, trees, rocks, and the like. What is emphasized is the recognition of another, not so much as a *thinker*, but as a *doer*. Remove this recognition and what you get is deception in the first or second category. This is not to suggest that intentional deception or proto-understanding of agency does not involve learning. They surely do; for instance, an animal may have to learn what class of things in its environment are agents rather than passive objects.

Put differently, in the first two categories the fact that the deceived party is an agent does figure in the story, but it makes no difference to the deceiving animal's behavior in genetic deception, and it underlies only discriminatory but still stimulus-bound and reinforced behavior in learned deception. Higher levels of deception, on the other hand, call for something extra, which is usually expressed in terms of the animal's understanding of the beliefs and desires of its target. But many types of flexible and forward-looking deception require only that the deceiver be able to predict the responses of the target, not necessarily that it understand the target's mental states.

What we call "proto-understanding of agency" is, then, roughly the capacity to have a rudimentary understanding of a causal relation between what another animal is perceiving at the moment (or perhaps even what it perceived a while ago) and how it is going to respond in a particular situation based on that perception (cf. Gomez 1991, Whiten 1997). It allows an animal to discriminate between agents, who do things in and to their environments, and objects, which do not act on their environments. This rudimentary understanding of causal agency can then be put to use in deceiving other animals, based on the recognition that a target animal, which is usually a conspecific, is *manipulable* in that its behavior, unlike the movements of inanimate objects, plants, and some other animals, will change depending on its perceptions.

In addition to proto-understanding of agency, we want to suggest a second building block for intentional deception: the ability to flexibly inhibit normal behavior that would result in immediate reward. This ability is important in allowing an animal to withhold informative signals or behavior. Although many animals can inhibit certain behaviors in a small set of contexts, we suggest that the flexibility of inhibition may be crucial in allowing certain types of deception to take place. Unfortunately, inhibition in naturalistic contexts has rarely been studied (cf. Diamond 1990, Hauser 2000), but it is likely that there are considerable variations. In the next section we describe one context where flexible inhibition may be crucial for deception.

A Test Case for Primate Deception: The Menzel Paradigm

We suggest that the abilities of proto-understanding of agency and flexible inhibi-

tion allow deceptive behaviors that go beyond stimulus-response learning, but need not involve the theory of mind abilities usually associated with intentional deception. By examining how different kinds of primates express these abilities in an experimental paradigm that tests for deception, we can begin to chart how a sophisticated cognitive ability such as (intentional) human deception is constituted of more elementary abilities found in other species.

To illustrate the relationship between proto-understanding of agency, inhibition, and deception, consider the Menzel paradigm, in which a subordinate animal is shown the location of a food cache and then the group (including a dominant animal) ignorant of the location is released with the subordinate (Menzel 1974; see also Hirata and Matsuzawa in review). When Menzel used this paradigm on chimpanzees, the dominant male followed the subordinate female to the food cache and took the food; he used her as a source of information. In the course of repeated trials, the subordinate began to take evasive actions; for instance, she would lead the group to a smaller food cache and then dart to the larger cache. But the dominant male soon ignored these tactics, and sometimes he even moved away from her, only to turn quickly to catch her heading for the food.

As described, each ape clearly recognizes, in some sense, how the other ape ''works'' (does things as an agent). At a minimum, they are able to predict the other's future behavior based on current perceptions and behavior. For example, the subordinate recognizes that if the dominant is attending to her movements and she goes to the food, she will lose it. He, in turn, recognizes that some of her movements are not reliable indicators of where the food is located, and he learns that she is more likely to reveal the food if she does not see him watching her.

The two key points in these experiments are that the apes' learning would require making complex and often novel connections between subtle bodily cues (e.g., gaze, body orientation) and future behavior, and second, the end result—no what matter what the ontogeny—is that the apes apparently recognize each other as agents perceiving and acting on their environments. Furthermore, each ape, because of the presence of the other, *inhibits* presumably powerful motivations to act as it normally would. The subordinate avoids moving toward a known food source; the dominant redirects attention away from a reliable indicator of food (i.e., the subordinate's movement). These behaviors represent a flexible type of inhibition driven, not by the presence of an aversive stimuli, but by a reward to be obtained at a later time. They are necessary for the deception and the counterdeception to occur.

In sum, the deceiving ape's behavior may not represent intentional deception with a theory of mind, but it probably involves cognitive abilities that outstrip those required for many types of merely learned behaviors. At the very least, the deceiver's behavior can be considered intentional in the sense that it has an intermediate goal to modify the perceptions or experience of the target ape so that its behavior is then altered (see Hauser 1997).

What's in a Lemur's Mind?

The Menzel paradigm has been replicated in a species of Old World monkey (mangabeys) that used some of the same tactics employed by the chimps; notably the subordinate explored several different tactics and learned to take indirect routes to the food or to wait until the dominant animal was preoccupied before going to the food (Coussi-Korbel 1994). We should note that the mangabeys did not necessarily perform deceptive behaviors as complex as those of the chimps, and some experiments suggest differences in the abilities of monkeys and apes to inhibit and to understand agency. However, here we focus on the differences in cognitive abilities demonstrated by strepsirhine primates and those demonstrated
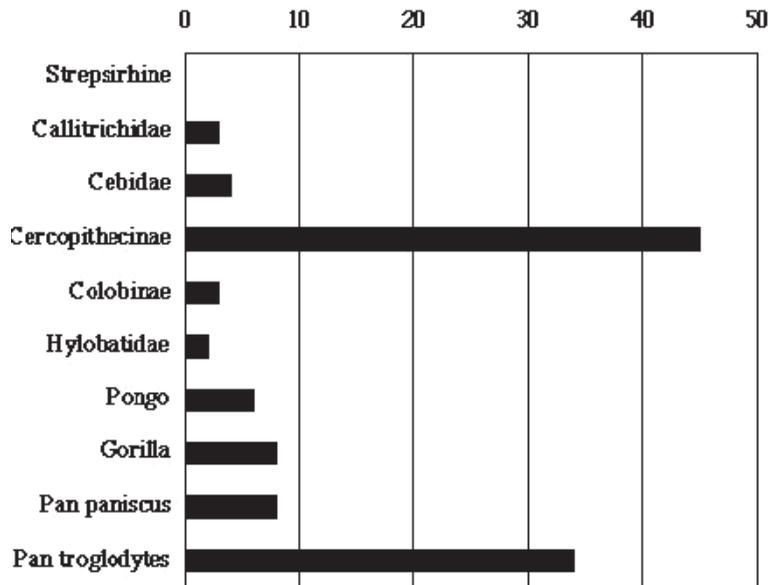
Figure 43.1
Taxonomic distribution of deception observations in primates (for details, see Byrne and Whiten 1992).

by both (some) monkeys and apes. The important point is that various types of deceptive behavior have been observed in most primate radiations, especially in baboons (cercopithecines) and chimpanzees, but no deception of any kind has been observed in any strepsirhine species (figure 43.1).

With this in mind, Robert Deaner replicated the Menzel paradigm with ringtailed lemurs at the Duke University Primate Center Durham, NC (Deaner 2000, in preparation).

In Deaner's setup (figure 43.2), a male ring-tailed lemur (the subordinate) was informed of the location of two grapes (the experimenter trained the lemurs to learn the location of the food by waving a towel in front of the correct location among eight possible sites), whereas a dominant female remained uninformed. Upon being released simultaneously into the foraging area, females regularly followed and displaced

the informed males and thus managed to obtain most of the grapes. Therefore the subordinate males had motivation to inhibit their movement toward the food location (just as the subordinate chimps and mangabeys did).

Even though this setup provided male ring-tailed lemurs with the opportunity to profit by deceiving females, deception was rare. For instance, in one representative dyad, a subordinate named Teres usually went directly to the site where he had observed the grapes hidden (as he did in baseline trials run alone), only to be followed by the dominant female, who took one or both of the grapes. Over many trials, however, Teres did employ several other tactics (table 43.1), and two of these even succeeded in deceiving the female and allowing Teres to gain both grapes without threat. Four times he departed from the trial shelter, waited for the female to move away from the baited site, and then pro-
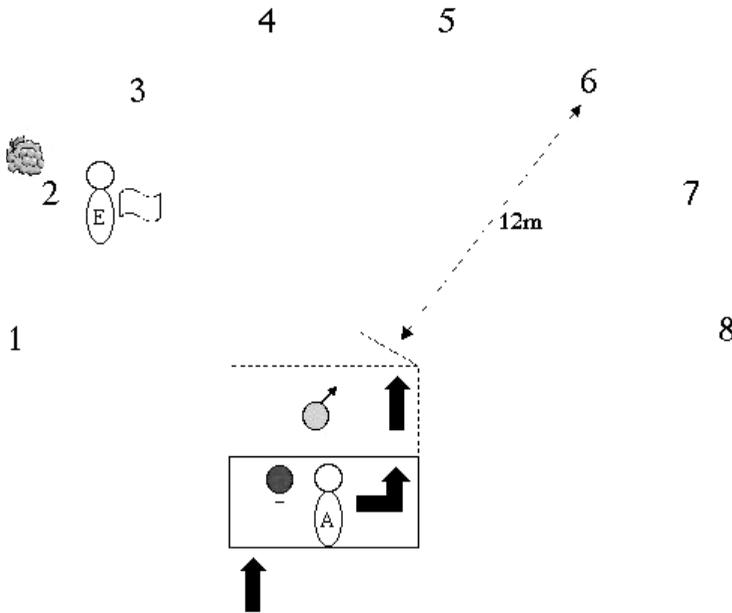
Figure 43.2
Experimental setup for study of ringtailed lemur deception. Male observes experimenter (E) waving towel to indicate location of grapes at feeding site 2. Meanwhile, female in trial shelter is monitored by assistant (A); after male is informed, female will be moved to the same part of the shelter as the male and the two lemurs will be released simultaneously.

ceeded to retrieve the grapes; twice he moved in the wrong direction, allowed the female to overtake him, and then moved to the correct site.

While these deceptive tactics were effective, Teres rarely used them, despite the fact that the female showed no indication of countering the deception by closely following Teres on the subsequent trial. Even more strikingly, across the 56 trials, and in subsequent trials with a second female, Teres did not begin using the deceptive tactics with increasing frequency. Thus there was no indication that he had learned what made the previous trial successful. In fact, in most dyads, after a male had previously been deceptive, in the next trial he usually proceeded directly to the baited site.

Although we cannot say for sure why male ringtailed lemurs do not practice deception more frequently in the Menzel paradigm, there are two likely possibilities. One is that, while the lemurs understand which behaviors are effective, they are unable to inhibit their tendency to go directly toward the food as soon as it is (apparently) accessible. This would explain why deceptive trials were frequently followed by direct dashes to the grapes. While an elementary understanding of agency (i.e., that behavior changes in response to what happens in one's perceived environment) is crucial to the ability to deceive, this understanding by itself, however sophisticated it may be, is ineffective in the absence of inhibition (whereas inhibition in the absence of understanding is

Table 43.1
Tactics employed by male ringtailed lemur, Teres, in a series of 56 dyadic trials with female, Adea

Description of Behavior	No. of Trials Used	Grapes/ Trial[a]	Tactic Classification
Depart immediately; move immediately in the correct direction; search baited site and nearby sites sequentially.	35	0.6 ± 0.7	Normal
Depart immediately; move immediately in the wrong direction; search unbaited site and nearby sites sequentially.	10	0.2 ± 0.6	Ineffective alternative
Wait in release cage; depart; move slowly to baited site.	2	0.5 ± 0.7	Ineffective alternative
Wait in release cage; depart; return to trial shelter for next trial (no search).	3	0.0 ± 0.0	Ineffective alternative
Depart immediately; wait (female moves in wrong direction); move to baited site.	4	2.0 ± 0.0	Effective alternative
Depart immediately; move immediately in wrong direction; stop at or before unbaited site (female searches unbaited site); move to baited site.	2	2.0 ± 0.0	Effective alternative

[a] Grapes per trial refers to the number of grapes Teres consumed per trial, out of a maximum of two.

useless). Supporting this possibility are data indicating that lemurs have more trouble than monkeys in an inhibition task where food must be obtained by initially pushing it away (Davis and Leary 1968).

Another possibility is that the lemurs cannot learn to associate their unusual behavior (i.e., their indirect route to the food) with a positive outcome (i.e., females moving away from the baited area). As we noted earlier, although associative learning is often thought of as a simple process, this is often not the case, especially when one must link, in particular contexts, events that rarely co-occur. In this case, the ability to associate the dominant's gaze and movements with her following behavior—that is, to have a proto-understanding of agency—could be extremely helpful and perhaps even necessary for deception.

Again there is some evidence for such a deficit in lemurs: Itakura (1996) and Anderson and Mitchell (1998) found that lemurs were less successful than monkeys and apes at co-orienting their visual gaze with humans, suggesting they did not recognize that gaze direction is indicative of future behavior. Thus perhaps lemurs fail the Menzel task, whereas monkeys and apes pass it, because lemurs lack one or both of the building blocks for intentional deception—the abilities to inhibit certain behaviors and to recognize how their conspecifics, as agents, are *deceivable*.

Conclusion

What lessons can we draw from this study, in the context of questions about animal cognition? To say that the differences among chimps, monkeys, and lemurs on the Menzel task show that the lemurs are simply less *intelligent* tells us nothing about what specific cognitive abilities may explain the differences in behavior; it is to use the word "intelligent" as a placeholder for a more robust future explanation. Similarly, in many cases animals are said to deceive one another without a clear enough understanding of the cognitive abilities that allow the apparently deceptive behavior. We need more fine-grained concepts and experimental tasks to understand how dif-

ferent kinds of deceptive behavior are possible for different species.

In the experiments described it is difficult to distinguish a lack of understanding of agency from a lack of inhibition. Nonetheless, these two ingredients of intentional deception can be examined separately, and possibly other cognitive constituents of deception can be conceptually characterized and empirically tested. This kind of research would help reveal the underlying components of intelligence and allow us to map out more precisely Darwin's continuum in the mental landscape of nature.

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