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Cooperation and deception in primates

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ABSTRACT

Though competition and cooperation are often considered opposing forces in an arms race driving natural selection, many animals, including humans, cooperate in order to mitigate competition with others. Understanding others' psychological states, such as seeing and knowing, others' goals and intentions, and coordinating actions are all important for complex cooperation—as well as for predicting behavior in order to take advantage of others through tactical deception, a form of competition. We outline evidence of primates' understanding of how others perceive the world, and then consider how the evidence from both deception and cooperation fits this framework to give us a more complete understanding of the evolution of complex social cognition in primates. In experimental food competitions, primates flexibly manipulate group-mates' behavior to tactically deceive them. Deception can infiltrate cooperative interactions, such as when one takes an unfair share of meat after a coordinated hunt. In order to counter competition of this sort, primates maintain cooperation through partner choice, partner control, and third party punishment. Yet humans appear to stand alone in their ability to understand others' beliefs, which allows us not only to deceive others with the explicit intent to create a false belief, but it also allows us to put ourselves in others' shoes to determine when cheaters need to be punished, even if we are not directly disadvantaged by the cheater.

1. Introduction

Practically any topic in social behavior revolves around the twin concepts of cooperation and competition (Alcock, 2001; Dugatkin, 2004; Hamilton, 1964; Krebs & Davies, 1997; Maynard Smith, 1982; Trivers, 1971). Although competition and cooperation are often described as opposing forces in an arms race driving natural selection, it is frequently the case that animals, including humans, cooperate in order to mitigate competition with others (Clutton-Brock, 2009; Muller & Mitani, 2005; Summers & Crespi, 2013). Evolution has addressed this dichotomy in different ways. In some cases, strategies have evolved that encourage cooperation, as exemplified by the eusocial insects (Holldobler & Wilson, 2008), with some castes of individuals producing few or no offspring, but spending their lives supporting their reproductive kin. This life history is highly cooperative but inflexible; no individual organism decides when, where, and with whom to cooperate. Other species, however, lack such biological enforcement mechanisms and therefore cooperation is more flexibly instantiated, involving strategic decision-making conditional on a partner's behavior (Brosnan, Salwiczek, & Bshary, 2010). While even flexible cooperation can be achieved without any understanding of the partner's psychological states, if cooperative partners can

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understand how each other perceives the world, and perhaps even the goals or intentions of the other, they can cooperate even more flexibly. Moreover, it is functionally advantageous to be able to anticipate others' future behavior in order to outmaneuver them, which requires the same cognitive mechanisms as are needed for this highly flexible cooperation (Whiten & Byrne, 1988). One key question in behavioral ecology, then, has been to try to determine when species cheat (we use the example of tactical deception as a form of competition), when they cooperate, and how they mitigate competition through cooperation.

Primates are particularly interesting to study from this perspective, as they are exceptional at social maneuvering. Primates keep track of social relationships, even in fission-fusion societies in which members aren't all present at the same time, form coalitions and alliances, and, it has been argued, tactically deceive one another (Byrne & Whiten, 1988; Chance & Mead, 1953; Cheney & Seyfarth, 1990a; Dunbar, 1998; Harcourt, 1992; Humphrey, 1976; Jolly, 1966; Kummer, 1967; Whiten & Byrne, 1997). It would be difficult to explain observations of primates flexibly adapting their behavior as their interactions progress without assuming social intelligence (Byrne, 1996; Humphrey, 1976). One challenge in this research, particularly (but not exclusively) with non-verbal species, is attempting to determine the degree to which primate behavior requires an understanding of basic perceptual (e.g., sight) and psychological states (e.g., knowledge, thoughts, beliefs, intentions, desire, etc.) (Cheney & Seyfarth, 1990b; Drayton & Santos, 2014; Fletcher & Carruthers, 2013; Premack & Woodruff, 1978; Seed & Tomasello, 2010; Whiten & Byrne, 1988; but see Heyes, 1998; Penn & Povinelli, 2007). Below we outline evidence of primates' understanding of how others perceive the world, and then consider how the evidence from both deception and cooperation fits this framework to give us a more complete understanding of the evolution of social cognition in primates.

2. Evidence that primates understand some perceptual and psychological states

Experimental evidence from a food competition paradigm demonstrates that primates understand some perceptual and psychological states of others, namely that others can see, hear, and have knowledge about events (reviewed in Whiten, 2013). In the paradigm, a lower-ranking individual knows the location of a hidden food and competes with naïve group-mates to find it. Not only do subjects react to their competitors' orienting behavior (chimpanzees *Pan troglodytes* spp., Hall et al., 2014), but they also show behavioral evidence of understanding what the competitor perceives or infers, for example, when the food is hidden behind a visual barrier (chimpanzees, Bräuer, Call, & Tomasello, 2007; Hare, Call, Agnetta, & Tomasello, 2000; Schmelz, Call, & Tomasello, 2011). Furthermore, some chimpanzee subjects actively conceal visual or auditory cues from competitors (e.g., human researchers in experimental studies; Hare, Call, & Tomasello, 2006; Melis, Call, & Tomasello, 2006a). Both monkeys and apes can also keep track of what others know based on what the others have seen, even if the item is out of view at the time of the competition (rhesus macaques *Macaca mulatta*, Flombaum & Santos, 2005; Santos, Nissen, & Ferrugia, 2006; chimpanzees, Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008). This evidence suggests that primates have abstract cognitive representation about some of their own (Hampton, 2009), and others' (Seed & Tomasello, 2010), psychological states.

Not only do primates react to others' overt behavior, they also understand others' goals, and in some cases, their intentions (Marsh & Legerstee, 2015). Primates react differently to human caretakers who are unwilling versus unable to give them food (chimpanzees, Call, Hare, Carpenter, & Tomasello, 2004; capuchins *Cebus apella*, Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009), and to humans who spill desired juice by accident versus on purpose (chimpanzees, orangutans *Pongo pygmaeus*, human children *Homo sapiens*, Call & Tomasello, 1998). In both scenarios, the behavior of the human and the outcome are the same, therefore the difference in response must be due to subjects' understanding of the contextual cues. Chimpanzees and capuchins are also able to recognize humans' goals to reach distant objects, and help them to access the items (capuchins, Barnes, Hill, Langer, Martinez, & Santos, 2008; chimpanzees, Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2008). This evidence suggests that some primate species are not responding based on dozens of learned associations, but are able to infer the outcomes of interactions from patterns that they observe, possibly through some intervening variable (e.g., the understanding of someone's goal or intention; Seed & Tomasello, 2010; Whiten, 1996, 2013).

3. Tactical deception as a form of competition

Byrne and Whiten (1988) defined tactical deception as "acts from the normal repertoire of the agent deployed such that another individual is likely to misinterpret what the acts signify, to the advantage of the agent." By definition, deception only works when rare (Dugatkin, Perlin, Lucas, & Atlas, 2005; Pruitt & Riechert, 2009; Ross-Gillespie, Gardner, West, & Griffin, 2007), therefore there are fewer observational examples than for many other behaviors, and experiments are challenging. One fruitful approach has been to collate researchers' observations of behavior that functioned deceptively (Byrne & Whiten, 1990) to serve as a starting point for more rigorous research (Byrne, 1997; McGrew, 2004; Sarringhaus, McGrew, & Marchant, 2005; Whiten & Byrne, 1988; but see Bernstein, 1988). One continued criticism of this approach is that observations of any sort can only demonstrate correlation, not causation. Thus although the sheer number of examples make it difficult to argue that there is not some behavior occurring that is at least functionally deceptive, it is impossible to determine the underlying level of intentionality. Therefore, researchers have begun to explore deceptive behavior experimentally.

Given primates' ability to understand how others perceive the world, and to understand others' goals, it would be functionally advantageous for them to predict others' behavior in order to manipulate it (Whiten & Byrne, 1988). Several studies