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In the hope of understanding more about the origins of human social cognitive abilities such as teaching and deception, much attention has been centered on the question of whether chimpanzees, our closest extant relatives, understand others as psychological agents (Tomasello and Call 1997; Tomasello 1999). Currently, results from work with chimpanzees can be viewed as contradictory (see Heyes 1998; Hare 2001). One approach, which represents the majority of studies, has produced little compelling evidence that chimpanzees attribute psychological states of any kind (i.e., perceptions, attention, intentions, or beliefs) to others (see Heyes 1998; Tomasello and Call 1997, for reviews). Another approach, by contrast, finds evidence that chimpanzees can at least take another individual's visual perspective (Hare et al. 2000; Hare et al. 2001; Hirata and Matsuzawa 2001).

There are two possible resolutions to these findings. The first is empirical; further experimental work may show that one or both approaches are flawed. The second is conceptual; theoretical differences that lead to different experimental paradigms may account for the different findings. Given that we do not know the outcome of future studies, we focus here on the second potential resolution. We ask whether seemingly contradictory experimental outcomes can be attributed to the types of problems that the two different approaches suggest should be posed to test species.

Attempts to understand the evolution of cognitive abilities are typically framed by one of two kinds of hypothesis, here called the "general-purpose intelligence hypothesis" and the "adapted cognition hypothesis." We argue that in order to improve our ability to design and interpret experiments on social cognition, it is most constructive to consider the predictions and approaches of both these hypotheses. We illustrate our argument with investigations into chimpan-

zee and dog social cognition. The results of these studies are puzzling and potentially contradictory in relation to the general-purpose intelligence hypothesis alone, but they make sense in light of the adapted cognition hypothesis.

The General-Purpose Intelligence Hypothesis

Models of general-purpose intelligence attempt to explain the evolution of all-purpose cognitive mechanisms such as memory, categorization, learning, or reasoning that can vary between genetically canalized systems, such as those often observed in invertebrates (Gould and Gould 1986), and highly flexible, content-independent cognitive processes believed to underlie human intelligence. The variation in the flexibility of these general-purpose problem-solving abilities is commonly considered to be explained by increases in computing power during evolution, rather than being the result of an adaptation to any particular kind of problem (Gibson 1990). An increase in general-purpose intelligence might evolve, for example, as a physiological constraint is released, allowing an increase in brain size and computing power (Aiello and Wheeler 1995).

Therefore, the general-purpose intelligence hypothesis predicts (1) taxon-level (or brain-sized) differences in intelligence that are unrelated to obvious features of ecology or social behavior and (2) abilities that can be applied across contexts and have not been selected to solve any specific evolutionary problem(s). Thus paradigms that can be used across taxa and that are evolutionarily irrelevant offer the most experimental power.

Examples consistent with these predictions include evidence for mirror recognition in several hominid species, but not in other primates (Galup 1982), and proposed taxon-level differences in reversal-learning tasks (Rumbaugh and Pate

1984a,b). In both cases, large-brained hominoid species, which evolved in radically different ecologies, outperform other primates in what are arguably evolutionarily irrelevant tasks.

The Adapted Cognition Hypothesis

In contrast, models of cognitive adaptation (e.g., domain specificity) assume that species evolve flexible mechanisms that function to solve particular kinds of ecological problems. Just as in the case of complex morphological or physiological adaptations, sophisticated cognitive adaptations are selected to solve the problems that an individual is most likely to encounter (Barkow et al. 1992). But cognitive adaptations are unlike other adaptations in that “evolution has relinquished its micromanagement of the behavioral interactions an organism has with its environment in deference to the individual and its judgment” (Tomasello and Call 1997, p. 9), allowing more flexible behavioral responses to ecological problems.

Thus the adapted cognition hypothesis predicts: (1) Since cognitive abilities have been selected to solve evolutionarily salient problems, a species’ most flexible cognitive abilities will be demonstrated in the settings for which these abilities evolved. (2) Variation in cognitive abilities among species will be explained by the different kinds of ecological problems the species has faced in its evolutionary history. Accordingly, tests of the adapted cognition hypothesis should be designed to echo the behavioral and ecological problems of that species’ evolutionary past.

The clearest examples of cognitive mechanisms being adaptations to a specific evolutionary history come from spatial tasks (see Hauser 2000 for a review). For example, bird species that cache food for later retrieval outperform those from closely related noncaching species. They also have a larger hippocampus, a structure involved in spatial memory (Balda and

Kamil 1989; Krebs et al. 1989). Clearly, ecological pressures favored caching ability, which selected for an enlarged hippocampus. As for experiments on animal social cognition, there seem to be few, if any, examples that support both of the predictions of the adapted cognition hypothesis.

Chimpanzee Behavior as a Guide to the Design of Experiments

In investigating the abilities of chimpanzees to attribute perceptions and beliefs to others, experimenters have used two approaches, utilizing different types of social problems. The classic approach utilizes a cooperative-communicative paradigm. In this paradigm, a human (and in one study a conspecific) shares information about the location of a monopolizable food resource that is hidden in a location the subject cannot see (Premack 1988; Povinelli et al. 1990, 1994, 1997, 1999; Tomasello et al. 1997; Call et al. 1998; Itakura and Tanaka 1998; Itakura et al. 1999; Call and Tomasello 1999; Call et al. 2000). In another version of the cooperative-communicative paradigm, a subject must signal to humans in some way in order to acquire a monopolizable piece of food (Premack 1988; Povinelli et al. 1992; Povinelli and Eddy 1996a,b; Reaux et al. 1999; Theall and Povinelli 1999). The alternative approach uses a competitive paradigm, in which socially housed chimpanzees compete with each other for food (Hare et al. 2000, 2001; Hirata and Matsuzawa 2001).

Given the different predictions of the general-purpose intelligence hypothesis and the adapted cognition hypothesis we outlined, it is vital to classify each of these experimental paradigms according to their evolutionary relevance. To do so, consider the frequency of cooperation and communication, and social competition, in the natural lives of chimpanzees.

Are there any natural analogs of the cooperative-communicative paradigm in wild chimpan-

zees? It is admittedly possible to imagine a natural event that mimics the social problem presented, where one individual needs information from a conspecific about hidden food. For example, imagine during a meat-eating episode that male *A* has a monkey carcass 15 m up in a tree. Next to him is a second male *B* who has no meat and is unsuccessfully begging for a piece from *A*. *A* sees one chunk of his meat, a leg perhaps, fall to the ground. As it falls, it bounces off a branch and flies leftward, so that only *A* sees where it lands. Can we expect *A* to share information about the location of the hidden food with *B*?

No. In Menzel's classic experiments in which a number of chimpanzees searched for hidden food, no informed individual ever spontaneously or overtly used communicative signals to indicate the location of hidden food to a conspecific (Menzel 1974). Chimpanzees systematically avoid sharing information about monopolizable food both in the wild (personal observation) and in captivity (Hauser and Wrangham 1987; Hauser et al. 1993). Because there appears to be no obvious parallel to this experimental setting in the wild, the cooperative-communicative paradigm is an excellent test of the general-purpose intelligence hypothesis since it appears to be so unnatural.

The social-competition paradigm, by contrast, presents chimpanzees with a problem they faced and solved on a daily basis over evolutionary time: outcompeting conspecifics for food. There are countless examples of food competition (see Goodall 1986). For example, lone individuals normally maintain an unchanged velocity as they approach a familiar fruit tree. However, when a party of chimpanzees approaches such a tree, they often break into a run at the last minute, and race to the preferred feeding spots (personal observation). In addition, there is much opportunity for the use of flexible strategies to out-compete competitors. For example, some chimpanzees can have greater knowledge than others about the location of food. Thus a party

approaching a fruit tree may include some who have fed from it daily for a week and others visiting for the first time. Therefore the knowledgeable chimpanzees could avoid informing ignorant individuals by using the best entrance routes or approaching the location with the highest density of fruit while they are unseen or while others are distracted. In addition, Goodall (1971) reports a number of observations in which a chimpanzee avoided food in the presence of ignorant but dominant competitors until they left. (In some cases they even proactively led the dominants away from the food.) In summary, chimpanzees regularly face problems of food competition, making it likely that their cognitive abilities function in part to solve these problems. The competitive paradigm is therefore a suitable choice for testing the adapted cognition hypothesis.

Testing the Adapted Cognition Hypothesis

Variation in Cognitive Ability According to Context

Experiments that utilize the cooperative-communicative approach have produced little compelling evidence for attribution of psychological states; these include tests of even the most basic social cognitive skills thought to be involved in human attribution (Povinelli 1996; Call et al. 2000). For example, in the object choice task, an experimenter hides food in one of two locations so that the subject knows the food is hidden, but does not know where. After baiting, the experimenter provides a social cue (eye direction, head direction, pointing, etc.) to indicate the location of the food to the subject. The question is whether the subject will use the cue provided by the human to find the hidden food. Most chimpanzees do not reliably use even the most obvious of cues, such as when the experimenter taps on the location of the food (Call et al. 1998, 2000). In addition, it takes many dozens of trials

for chimpanzees to use an arbitrary and novel cue (such as a wooden block on the correct container) to find hidden food (Tomasello et al. 1997).

In contrast, experiments that utilize the competitive approach have produced promising results. Hare et al. (2000) baited an arena between the rooms of two chimpanzees with two pieces of food. As expected, in the control condition when two pieces of food were placed in view of both competitors, the dominant subject retrieved most of the food. If one piece of food was hidden from the dominant behind an occluder while the subordinate could see both pieces, as subordinates, the subjects preferred to retrieve the hidden piece of food that the dominant could not see. In contrast, if one piece was hidden from the subordinate behind an occluder, but the dominant could see both pieces, as dominants, the subjects preferred to retrieve the visible piece of food first to ensure that they obtained both pieces.

Hare et al. (2001) adapted the same competitive paradigm to test what chimpanzees know about what others have and have not seen in the immediate past in a number of situations. In experimental conditions, subordinates saw where food was hidden and that their dominant competitor did not. In control conditions, subordinates saw where food was hidden as the dominant watched. Subordinates preferred to retrieve food in experimental conditions. In addition, they refused to even approach more often in control conditions. Finally, in corroboration, Hirata and Matsuzawa (2001) found that during competition over hidden food, chimpanzees tend to use the behavior of competitors when they have seen food hidden, but ignore the behavior of ignorant individuals who have not seen food hidden.

Taken together, these findings demonstrate that chimpanzees know what conspecifics do and do not see, and furthermore, that they use this knowledge to develop flexible behavioral strategies in a number of different competitive situations. Most important, the combined results of

these two approaches are consistent with the first prediction of the adapted cognition hypothesis. Chimpanzees' social cognitive skills seem to be most flexible and sophisticated when solving the problems that this species faced during their evolutionary history.

Variation in Cognitive Ability According to Evolutionary History

The second prediction of the adapted cognition hypothesis is that different species will have different social cognitive abilities, which are correlated with the problems they faced in their evolutionary history. To take an example contrasting sharply with chimpanzees, dogs have evolved to cooperate and communicate with humans (Scott and Fuller 1967; Serpell and Barrett 1996). Accordingly, we expect that this species will show skills in the cooperative-communicative tasks that chimpanzees do not.

In the object choice task, dogs clearly can use a number of social cues provided by humans to find hidden food, including distal pointing and gaze direction (Miklosi et al. 1998; Mckinney and Sambrook 2000). But how flexibly can they use these social cues? Hare et al. (1998) and Hare and Tomasello (1999) ruled out the possibility that dogs were simply using the direction of their informant's movements as a cue. In addition, Hare and Tomasello (1999) found that whether it was an unfamiliar human or another dog, the identity of the informant had no effect on performance. Finally, unlike chimpanzees, adult dogs and puppies immediately used a novel and arbitrary cue to find hidden food (Agnetta et al. 2000).

Meanwhile wolves, the direct ancestors of dogs, who have not been selected to engage in cooperative-communicative interactions with humans, do not use social cues such as tapping, pointing, or head movement provided by an experimenter (Agnetta et al. 2000; Hare et al. submitted). Thus, the abilities of domestic dogs relative to primates and wolves in the object

choice task supports the second prediction of the adapted cognition hypothesis that variation in social cognitive abilities is explained by variation in the problems presented in the past by different social-ecological contexts.

An Integrated Approach for Studying Social Cognition

The general-purpose intelligence hypothesis and the adapted cognition hypothesis are not necessarily mutually exclusive. For example, Tomasello and Call (1997) proposed that the ability of primates to understand tertiary relationships evolved first in the social domain and was later extended to the physical domain as well. Nevertheless since the two hypotheses have different implications, it is important to consider them separately.

First, if the adapted cognition hypothesis is right, the relationship of the experimental paradigm to the test species' evolutionary history affects the interpretation of results. Thus if a cognitive ability is found to be absent in an ecologically irrelevant experimental context, the result represents a good test of the predictions of the general-purpose intelligence hypothesis, but not of the adapted cognition hypothesis. Further experiments would be needed to test the predictions of the adapted cognition hypothesis.

Second, the adapted cognition hypothesis helps predict where cognitive flexibility and sophistication are most likely to reside (Barkow et al. 1992). If tests designed on this basis are successful, novel (ecologically irrelevant) problems can be introduced to test the general-purpose intelligence hypothesis. For example, to test for coordinated cooperation, Hare (2001) suggested an experiment in which two chimpanzees must work together in a physical task to outcompete a third, since the majority of cooperative interactions occur in attempts to outcompete third parties (Harcourt and de Waal 1992). If individuals showed coordination in this paradigm, then

they could subsequently be tested in a novel noncompetitive version of the same task.

Unfortunately, there are no truly objective methods for operationalizing the evolutionary relevance of different paradigms. This makes careful consideration of a test species' ecology even more important in experimental designs and suggests that solving this problem is a priority for experimentalists (Hare 2001).

Finally, the relative importance of the two hypotheses in explaining the evolution of social cognition will be most easily assessed by testing a wider variety of species. Only by considering a wide range of species can one expect to find variation in cognitive abilities that corresponds with ecological differences (Burghardt and Gittleman 1990). For example, tamarins (Callitrichidae) have evolved as cooperative breeders, with adults being aided by juveniles in raising offspring. Tamarin helpers catch prey and can even give a food call that summons the young, to whom they give the food (Goldizen 1987). This suggests that unlike other primates, tamarins might demonstrate more flexibility in cooperative paradigms than in competitive paradigms (at least in those that involve food).

Experiments designed to test such ideas will therefore require comparative psychologists to work closely with behavioral ecologists. The results should clarify the evolutionary relationship between general-purpose intelligence and adapted cognition, both of which appear to play an important role in mammalian cognition. They will also raise fascinating questions about the mechanisms that limit a species' ability to solve social-cognitive problems that are posed in evolutionarily novel contexts.

Acknowledgments

We wish to thank the editors for inviting us to contribute. In addition, we wish to thank them for their valuable comments and Marc Hauser, Sonya Kahlenberg, Matthew McIntyre, Cory

Miller, Katarina Mucha, Michael Tomasello, and Michael Wilson for comments provided on an earlier version of this manuscript.

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This is a section of [doi:10.7551/mitpress/1885.001.0001](https://doi.org/10.7551/mitpress/1885.001.0001)

The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

Edited by: Marc Bekoff, Colin Allen, Gordon M. Burghardt

Citation:

The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition

Edited by: Marc Bekoff, Colin Allen, Gordon M. Burghardt

DOI: 10.7551/mitpress/1885.001.0001

ISBN (electronic): 9780262268028

Publisher: The MIT Press

Published: 2002

The open access edition of this book was made possible by generous funding and support from Arcadia – a charitable fund of Lisbet Rausing and Peter Baldwin



The MIT Press

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This book was set in Times New Roman on 3B2 by Asco Typesetters, Hong Kong. Printed and bound in the United States of America.

Library of Congress Cataloging-in-Publication Data

The cognitive animal: empirical and theoretical perspectives on animal cognition /
edited by Marc Bekoff, Colin Allen, and Gordon M. Burghardt.

p. cm.

“A Bradford book.”

Includes bibliographical references.

ISBN 0-262-02514-0 (hc. : alk. paper)—ISBN 0-262-52322-1 (pbk. : alk. paper)

1. Cognition in animals. I. Bekoff, Marc. II. Allen, Colin. III. Burghardt, Gordon M.,
1941—

QL785 .C485 2002

591.5'13—dc21

2001057965