Animal Behaviour xxx (2015) 1–12

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Special Issue: Social Evolution

Social cognition

Robert M. Seyfarth [a,*], Dorothy L. Cheney [b]

[a] Department of Psychology, University of Pennsylvania, Philadelphia, PA, U.S.A.
[b] Department of Biology, University of Pennsylvania, Philadelphia, PA, U.S.A.

ARTICLE INFO

Article history:
Available online xxx

MS. number: SI-14-00909

Keywords:
evolution
fitness
future research
personality
selective pressure
skill
social cognition

The social intelligence hypothesis argues that competition and cooperation among individuals have shaped the evolution of cognition in animals. What do we mean by social cognition? Here we suggest that the building blocks of social cognition are a suite of skills, ordered roughly according to the cognitive demands they place upon individuals. These skills allow an animal to recognize others by various means; to recognize and remember other animals' relationships; and, perhaps, to attribute mental states to them. Some skills are elementary and virtually ubiquitous in the animal kingdom; others are more limited in their taxonomic distribution. We treat these skills as the targets of selection, and assume that more complex levels of social cognition evolve only when simpler methods are inadequate. As a result, more complex levels of social cognition indicate greater selective pressures in the past. The presence of each skill can be tested directly through field observations and experiments. In addition, the same methods that have been used to compare social cognition across species can also be used to measure individual differences within species and to test the hypothesis that individual differences in social cognition are linked to differences in reproductive success.

The social intelligence hypothesis, originally proposed by Chance and Mead (1953), Jolly (1966) and Humphrey (1976), argues that selective pressures imposed by the social environment, specifically, competition and cooperation with conspecifics, have played an important role in shaping the evolution of the brain and cognition in animals. But what, exactly, do we mean by 'social cognition'? Here we discuss the mechanisms that underlie social cognition, and how they can be measured and compared across both species and individuals. Our goal is to quantify levels of social cognition, to show how cognitive complexity can be tested among free-ranging animals, and to discuss the potential links between social cognition and fitness.

In her original formulation, Jolly (1966) was struck by the fact that many primates, like the ringtailed lemurs, *Lemur catta*, she studied, exhibit complex societies, differentiated social relationships and extensive social learning 'but lack much capacity to learn about objects' (1966, page 506). She concluded that 'social life preceded, and determined the nature of, primate intelligence' (1966, page 506).

In practice, however, it is difficult to place a strict dividing line between 'social' and 'nonsocial' cognition, for at least two reasons. First, among group-living animals, many interactions with the nonsocial environment have a social component. Memory of the location and timing of fruiting trees, for example, or the boundaries of a large home range, are formed as a group moves through its habitat, with some individuals leading, others following, and all animals presumably learning from each other as they go. As a result, while laboratory studies may try to separate social and nonsocial performance in their analysis of the factors that have shaped brain evolution (e.g. Genovesio, Wise, & Passingham, 2014), under natural conditions it is often difficult to do so. Second, as Bond, Wei, and Kamil (2010) noted, the ability to remember nonsocial stimuli (e.g. location of cached food) or social stimuli (e.g. a dominance hierarchy) may be governed by many of the same underlying general mechanisms, making it difficult to distinguish whether skills in modern species have arisen through social or nonsocial pressures. Consistent with this view, measures of cognitive skill in primates are correlated across multiple domains (e.g. behavioural innovation, social learning, tool use and extractive foraging), suggesting that 'social, technical and ecological abilities have coevolved' (Reader, Hager, & Laland, 2011, page 1017; see also Holekamp, Dantzer, Stricker, Yoshida, & Benson-Amran, 2015, this issue).

We begin, therefore, with a disclaimer: when we talk about social cognition we are not claiming that selection has not acted on individuals' knowledge of other environmental features (for reviews see e.g. Morand-Ferron, Cole, & Quinn, 2015; Reader et al.,

* Correspondence: R. M. Seyfarth, Department of Psychology, University of Pennsylvania, Philadelphia, PA 19104, U.S.A.
E-mail address: seyfarth@psych.upenn.edu (R. M. Seyfarth).

http://dx.doi.org/10.1016/j.anbehav.2015.01.030

Please cite this article in press as: Seyfarth, R. M., & Cheney, D. L., Social cognition, Animal Behaviour (2015), http://dx.doi.org/10.1016/j.anbehav.2015.01.030

2011; Thornton & Lukas, 2012), nor do we support 'an exclusively social model of primate intelligence' (Reader et al., 2011, page 1017). Instead, we focus on the fact that all group-living animals confront a multitude of social problems, and that some aspects of cognition may have evolved at least in part because selection has favoured individuals who are skilled and motivated to solve them (Cheney & Seyfarth, 2007). Social cognition, moreover, can be quantified and tested experimentally, both across and within species. Our focus on social problems may also help to redress an imbalance: in a recent forum on the evolution of cognition in animals (Rowe & Healey, 2014, plus commentary replies) studies of social cognition are barely mentioned.

We define social cognition as knowledge about conspecifics, and we measure the complexity of social cognition by measuring the complexity of individuals' knowledge of their own and other animals' social interactions and relationships. Our focus is on those aspects of cognition that can be attributed, wholly or in part, to selection acting within the domain of conspecific interactions. It remains an open question whether the social environment presents animals with problems that are formally different or more complex than those presented by other stimuli.

PREVIOUS APPROACHES

Several studies have used experiments to quantify social cognition and test the hypothesis that individuals living in more complex societies should exhibit greater cognitive skills, at least in the social domain. For example, Bond, Kamil, and Balda (2003) compared the performance of highly social pinyon jays, *Gymnorhinus cyanocephalus*, and much less social western scrub-jays, *Aphelocoma californica*, on tests of transitive inference. They found that the pinyon jays' performance was superior to that of the scrub-jays, supporting an association between social complexity and cognitive skill (see also Paz y Miño, Bond, Kamil, & Balda, 2004). Similarly, Hick, Reddon, O'Connor, and Balshine (2014) compared contest behaviour in four species of cichlid fish. Two were pair-breeders, one was group living and highly social, and a fourth was solitary. They found that individuals in highly social species were better at discriminating between familiar and unfamiliar individuals, had shorter contests with fewer aggressive acts and resolved contexts more peacefully than individuals in other species. They concluded that skills in resolving conflicts 'are fundamentally linked to the evolution of complex social systems' (2014, page 47; see also Sandel, MacLean, & Hare, 2011).

In other studies, scientists have varied the complexity of the social environment experienced by immature animals, then tested the effect of this manipulation on adult social skills. Arnold and Taborsky (2010), for instance, raised cichlid fish (*Neolamprologus pulcher*) with either adults or alone. They hypothesized that those reared with adults would experience a more complex social environment, and they found that, in subsequent social tests, these individuals exhibited greater skill and success in their interactions with others as compared with peer-raised individuals (see also Kotrschal, Rogell, Maklakov, & Kolm, 2012; Kotrschal & Taborsky, 2010). In a study of cowbirds (*Molothrus ater*), White, Gersick, Freed-Brown, and Snyder-Mackler (2010) created two types of flocks that differed in social complexity. In 'dynamic' flocks, birds regularly moved between groups, whereas in 'stable' flocks, membership remained constant throughout the year. When males from the two conditions were placed in new environments with unfamiliar females, the dynamic-condition males had higher reproductive success.

These experiments offer a promising approach to studies of social cognition because they involve direct, experimental tests and focus on specific skills that are potentially linked to reproductive success. Although they cannot yet reveal whether differences in adult behaviour are due to differences in cognitive skill or some other factor, they permit direct comparisons both across species and across individuals within a species.

However, while experiments that manipulate group size, composition and social experience can readily be conducted on insects, fish and birds, they are difficult if not impossible to conduct on larger, long-lived and free-ranging mammals like hyaenas, dolphins, elephants and nonhuman primates. These species are of particular interest because they have large brains and complex societies. With this limitation in mind, we highlight below some different, complementary methods that lend themselves to field studies of large mammals and focused experimentation. These methods allow direct comparisons of social cognition across species and individuals. They may also allow tests of the hypothesis that individual differences in cognitive skill are linked to differences in reproductive success.

As an organizing framework, we propose that the building blocks of social cognition are a suite of skills, ordered roughly according to the cognitive demands they appear to place upon individuals. These skills allow animals to recognize individuals by various means, remember past interactions, observe others, recognize their social relationships and attribute mental states to them.

We treat these building blocks of social cognition as targets of selection. We assume that they are adaptive because they allow individuals to predict other animals' behaviour and intentions, to succeed in competitive encounters, and to form and maintain beneficial social bonds. We hypothesize that more complex levels of social cognition evolve only when simpler methods are inadequate and that, as a result, more complex levels of social cognition indicate greater selective pressures in the past (Cheney & Seyfarth, 2007; Humphrey, 1976; Wiley, 2013). Some skills are elementary and virtually ubiquitous in the animal kingdom; others are more complex and more limited in their taxonomic distribution. Exactly how the various skills are distributed across species and individuals remains an empirical question.

The building blocks of social cognition can be tested directly through field observation and experiments. We discuss some of these experiments in Part 1. In Part 2 we argue that the same methods can also be used to measure individual differences within a species and to test the hypothesis that individual variation in social cognition is linked to variation in reproductive success. The skills we describe are of broad scientific interest because of their close relation to many of the mental processes that play central roles in neuroscience and cognitive science. Finally, in Part 3 we discuss some avenues for future research.

Our method borrows from that used in the comparative study of animal navigation, where a recent review concludes as follows:

> *Comparing across a range of species whose navigational competence varies from simple to sophisticated, we note that complex and more phylogenetically recent abilities appear to be synthesized from simple, phylogenetically older ones. Using the observation as a starting point, we organize … navigational behaviours loosely into a hierarchical framework — the navigation toolbox — which is a collection of processes that can support, either alone or collectively, navigational behaviours of varying complexity.* **(Wiener et al., 2011)**

Our goal is not a complete review of the literature on tests of social cognition. Instead, our aim is to suggest ways in which social cognition can be quantified, tested experimentally on free-ranging animals, and compared across species and individuals, thereby offering tests of the social intelligence hypothesis that complement and extend existing methods.

Please cite this article in press as: Seyfarth, R. M., & Cheney, D. L., Social cognition, Animal Behaviour (2015), http://dx.doi.org/10.1016/j.anbehav.2015.01.030