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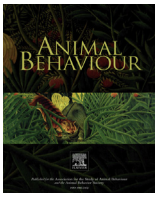

Special Issue: Unasked Questions

On understanding the nature and evolution of social cognition: a need for the study of communication

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Social cognition involves a wide range of processes, including the ability to recognize group members, to remember past interactions with them and to influence their behaviour strategically. Key arguments and findings in studies of the evolution of social cognition revolve around individuals flexibly and adaptively influencing the behaviour of others. One of the most effective ways of influencing the behaviour of others is through communication. Curiously, however, research focused on the evolution of social cognition rarely addresses communication in the species being studied. Here we describe four major hypotheses to explain the evolution of social cognition and, for each, raise specific predictions regarding communication and how it relates to social cognition. We argue that because communication is foundational to social cognition, studies of communication should be a core feature of future work on the evolution of social cognition.

Individuals of social species live in complicated social worlds. Navigating the social world is difficult because the social world is inherently reactive (or reflexive; see Leydesdorff, Petersen, & Ivanova, 2017). The behaviour of one individual affects the behaviour of others, which can in turn affect that first individual. Complex social dynamics occur even in small groups, as has been known in human psychology for decades (Hare, Borgotta, & Bales, 1955). For example, a group as small as four individuals has considerable combinatorial complexity in the number of possible social interactions and social behavioural decisions that each individual can make (Shubik, 1998). Thus, as social groups increase in complexity, there should be pressure for greater social cognition in those groups.

What does it mean for social groups to ‘increase in complexity’? Although there is a tendency to think of variation in social complexity in discrete terms (e.g. social versus solitary, complex versus simple), ‘complexity’ is a continuous feature of the social world. Compared to simple groups, groups that are relatively complex generally have more individuals, a greater diversity of individuals and a larger number of different types of relationships among individuals (Bergman & Beehner, 2015; Fischer, Farnworth, Sennhenn-Reulen, & Hammerschmidt, 2017; Freeberg, Dunbar, & Ord, 2012; Page, 2011; see also Hobson et al., this issue). Although group size is often a practical and straightforward proxy of social complexity, it may not be the most appropriate one in some systems. This point above on the nature of relationships among group members is crucial to notions of complexity, as very large assemblages of animals (such as blackbird flocks or bison herds of perhaps several thousand individuals) do not possess the relationships among individuals that are key to social complexity (Bergman & Beehner, 2015). Compared to simpler groups, then, individuals in more complex groups with networks of diverse

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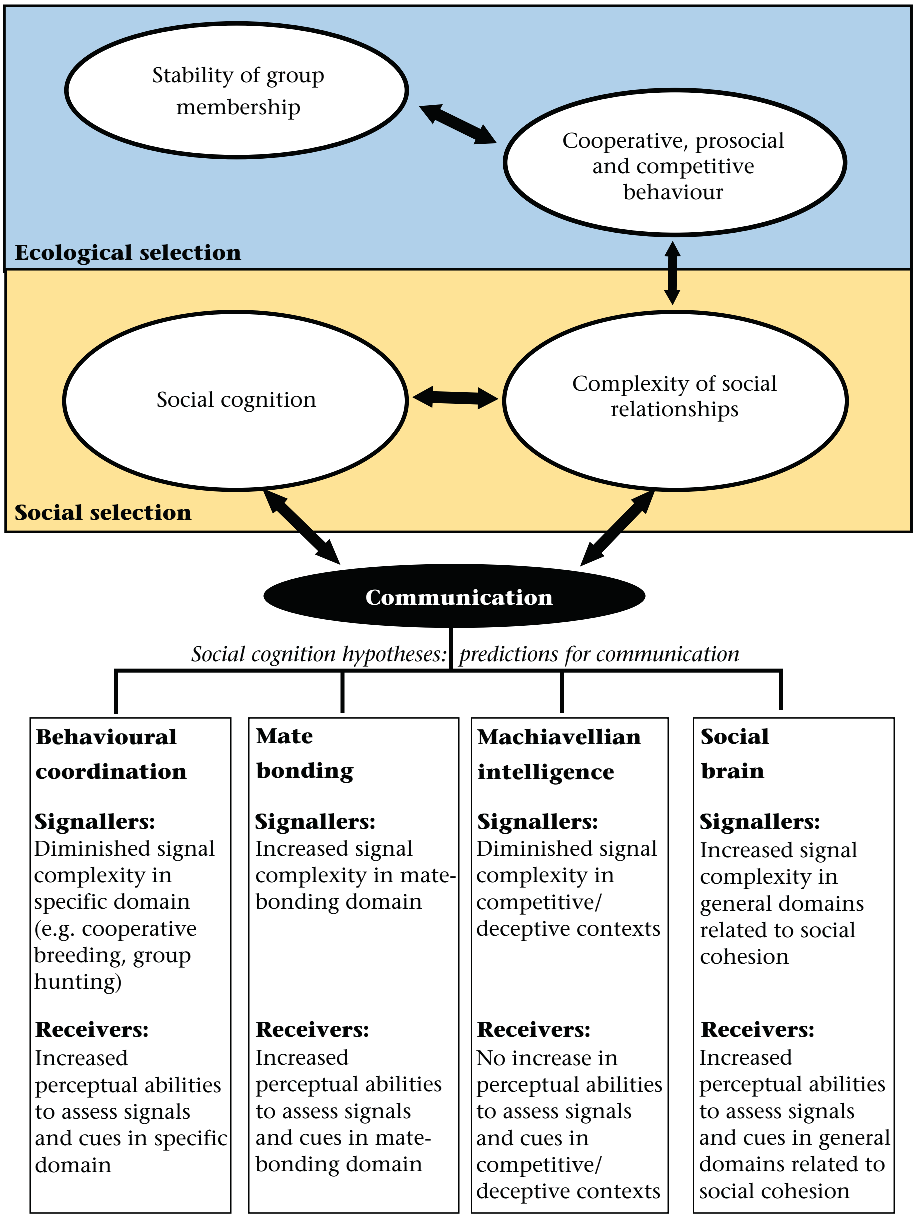
relationships face considerable social entropy – with less predictability as to the next individual with which to interact and the type of interaction that might occur (Whiten, 2000). Moreover, complex social systems embody greater uncertainty about the affective or cognitive states of group members, including their behavioural motivations and potential responses.

Early discussion of social complexity selecting for increased cognitive ability focused on two sides of sociality: (1) the cohesive and prosocial aspects of sociality (Jolly, 1966) and (2) the cooperative and the competitive/deceptive aspects of sociality (Humphrey, 1976). Increased social cognition enhances an individual's ability to behave in a coordinated and potentially cooperative way with one's group, but also to act competitively when it is to one's advantage. This basic notion about social cognition relates to problem-solving abilities in the social domain. Individuals must be able to gather social knowledge effectively – the awareness of the social states and conditions of others in their group (Byrne & Whiten, 1988). Social knowledge facilitates dominance hierarchies, social bonds, cooperation, competition and the organizing of social groups. Thus, an individual's ability to process information about – and to act effectively to influence – the likely behaviour of other individuals is paramount (Bradbury & Vehrencamp, 2011; Owings & Morton, 1998).

Effective social living thus requires social cognition. Social cognition comprises diverse processes such as recognizing group members, remembering past interactions with them and influencing their behaviour strategically (Olmstead & Kuhlmeier, 2015; Shettleworth, 2010). Variation in social cognition across species is thought to correlate with variation in social group complexity (Byrne & Whiten, 1988; de Waal & Tyack, 2003; Shultz & Dunbar, 2007; Whiten & Byrne, 1997; but see ; Barrett, Henzi, & Rendall, 2007). Key to the evolution of social cognition is the ability of



	Behavioural coordination	Mate bonding	Machiavellian intelligence	Social brain
Signallers:	Diminished signal complexity in specific domain (e.g. cooperative breeding, group hunting)	Increased signal complexity in mate-bonding domain	Diminished signal complexity in competitive/ deceptive contexts	Increased signal complexity in general domains related to social cohesion
Receivers:	Increased perceptual abilities to assess signals and cues in specific domain	Increased perceptual abilities to assess signals and cues in mate-bonding domain	No increase in perceptual abilities to assess signals and cues in competitive/ deceptive contexts	Increased perceptual abilities to assess signals and cues in general domains related to social cohesion

Figure 1. Ecological and social selection pressures influencing social cognition and communication (adapted from Crook, 1988). The four hypotheses to explain the evolution of social cognition are described in greater detail in Dunbar and Shultz (2017); unique predictions of each for variation in communication are found in the boxes at the bottom of the figure.

individuals to flexibly and adaptively manage and manipulate the behaviour of others. Perhaps the most effective way of doing so is through communication (Bradbury & Vehrencamp, 2011). Thus, species with complex social groups should have complex systems of communication, providing individuals diverse behavioural ways to assess and manage the behaviour of group members (Cheney & Seyfarth, 2018; Dunbar, 2003; Freeberg et al., 2012; Peckre, Kappeler, & Fichtel, 2019). Curiously, however, research on the evolution of social cognition has rarely addressed the issue of communication. We argue that studies of communication should be a core feature of future work on the evolution of social cognition.

We have given a brief overview of general arguments about the nature and evolution of social cognition in species with complex social groups. Certain ecological conditions (e.g. the relative distribution of predators and food) select for stability of group membership in space or time (or both), which facilitates both competitive and cooperative behaviour among group members (Fig. 1; Crook, 1988). Such behaviour necessarily influences the complexity of social groups and, in turn, social cognition, resulting in bidirectional social selection pressures affecting individuals in those groups. Below we develop the argument that communication is fundamental to social cognition, we briefly assess four major hypotheses to explain the evolution of social cognition, and we offer key predictions for each hypothesis that emerge regarding communication (Fig. 1; see also Dunbar & Shultz, 2017).

COMMUNICATION AND SOCIAL COGNITION

All living things communicate (e.g. Babikova et al., 2013; Diggle, West, Gardner, & Griffin, 2008; Schaefer & Ruxton, 2011). Communication involves an action or characteristic of one individual that influences the behaviour, behavioural tendency or physiology of at least one other individual in a fashion typically adaptive to both (Bradbury & Vehrencamp, 2011; Wilson, 1975). The first individual is called a sender or signaller, and individuals affected by the communicative act are called the receivers or audience. Note that the receiver can derive additional information about the sender through its cues. A signal is a feature of the sender that communicates something to a receiver and that has evolved for that communicative purpose, whereas a cue is a feature of the sender that communicates something to a receiver as an incidental by-product of its normal activities and did not evolve for that communicative purpose (Maynard Smith & Harper, 2003).

Signals and cues probabilistically predict states or activities of the sender that can be important for the receiver to know. Receivers continually update their understanding of the world based upon their own previously acquired information, but also upon the information they gain from the signals and cues of senders (Kight, McNamara, Stephens, & Dall, 2013). Receivers attend to senders' signals and cues because they are associated with functionally important variation in characteristics of the sender, the environment, or both.

Two classic publications in animal communication have become centrepieces of current debates and thinking about communication (Stegmann, 2013). In 1977, Eugene Morton described 'motivational-structural rules' for vocal communication, which laid the groundwork for what has become known as the 'assessment/management' approach to communication (Morton, 1977). In the same year, W. John Smith (1977) published *The Behavior of Communicating: an Ethological Approach*, where he described various displays of species, the messages and meanings of those displays and the contexts in which they are given. Smith relied heavily on an 'informational' approach to communication, an approach criticized by the assessment/management framework. Despite their theoretical and semantic differences, however, Morton and Smith raised similar issues linking complexity of social groups to complexity of communication systems used by individuals in those groups. We can think about communicative complexity in a parallel manner to the description of social complexity raised above. Compared to relatively simple communication systems, complex communication systems have a large and diverse number of signals (calls, songs, displays, etc.) that can be combined into yet more complex combinations and sequences (Kershenbaum et al., 2016; Lucas, Gentry, Sieving, & Freeberg, 2018) that can potentially be used to communicate a wider range of social motivations and behavioural tendencies.

As we discussed above, adaptive social living requires social cognition. Species in which individuals typically occur in more complex social groups have more sophisticated social cognition in comparison to species in which individuals typically occur alone or in fairly simple social groups (Shultz & Dunbar, 2007). Part of this increased social cognition includes effective signalling abilities as well as sophisticated perceptual abilities to process signals and cues from other individuals. Indeed, sustained social interaction would be impossible without the ability to signal flexibly and to perceive signals and cues of others effectively (Cheney & Seyfarth, 2018; Freeberg et al., 2012; Peckre et al., 2019; Sewall, 2015). It is also important to consider the different ways in which signals and signalling systems can vary in communicative complexity. For example, comparative work in ground-dwelling sciurid rodent species has found that increases in group size are associated with increases in individuality (across-individual distinctiveness) in alarm calls, but increases in diversity of social roles within groups are associated with increases in alarm call repertoire size (reviewed in Pollard & Blumstein, 2012). Some of these different ways in which signals and signalling systems can vary, furthermore, trade off with one another. As one example, strong selection for individuality in signal characteristics comes at the expense of possible 'signatures' of group-level signalling distinctiveness.

COMMUNICATION AND THE EVOLUTION OF SOCIAL COGNITION

A general view in the field of comparative social cognition is that individuals in species with complex social groups require greater cognitive abilities in the social domain than individuals in species with simpler social groups (see Shultz & Dunbar, 2007). However, there are different hypotheses to explain how pressures from complex social groups might drive increased social cognition in individuals. These hypotheses were discussed recently in a review of the evolution of brain size (Dunbar & Shultz, 2017), although there is clearly more to social cognition than absolute or relative brain size (Healy & Rowe, 2007, 2013). Using the framework from the Dunbar and Shultz (2017) review, we briefly summarize each hypothesis and discuss for each the importance of communication (Fig. 1).

Behavioural Coordination Hypothesis

A number of separate hypotheses relate broadly to the need for coordination of activities among individuals in socially complex groups (together called the 'behavioural coordination hypothesis'; called the 'cultural intelligence hypothesis' in Dunbar & Shultz, 2017). Three general views are expressed in these hypotheses. One view holds that the social learning of behaviour through processes like imitation is the key driver of the evolution of enhanced machinery for social cognition (Reader, Hager, & Laland, 2011; van Schaik, Isler, & Burkart, 2012). In imitation, one individual must effectively perceive the movements or signals (e.g. for vocal imitation) of a second individual if the correct behaviour pattern is to be copied (Goodale & Kotagama, 2006; Whiten & Custance, 1996). A second view holds that cooperative breeding imposes stronger pressures on individuals to process signals and cues of others compared to noncooperative breeding (Burkart, Hrdy, & van Schaik, 2009). In cooperative breeding, the effective raising of young requires coordinated activities with minimal conflict (Koenig & Mumme, 1987). A final view holds that social hunting predators require more sophisticated processing of social information compared to predators that hunt alone (Beauchamp, 2014; Kershenbaum & Blumstein, 2017; Smith, Swanson, Reed, & Holekamp, 2012). Socially hunting predators often take large prey that could not otherwise be subdued. These attacks often require interindividual coordination facilitated by a cognitive sophistication unnecessary in nonsocially hunting species.

Although these examples represent different behavioural systems or behavioural contexts (learning, parental care and foraging), they share the notion of individuals needing to attend intensively to the behaviour of others, to influence the behaviour of others effectively (and often quickly) in the specific domain requiring coordination, or both. Under this behavioural coordination hypothesis, we would expect relatively little signal diversity for signals produced in the specific domain (e.g. hunting, nest switching, etc.), as signals in these domains would be expected to be highly context specific. Signals in these domains should be selected to be stereotyped, unambiguous and highly salient to receivers. We might expect increased individual-level distinctiveness in signals in coordination related to social hunting, however, in that context alone would not reliably provide information about signaller identity in space and time. We would furthermore expect variation in communicative complexity outside the specific domain of behavioural coordination (whether social learning, cooperative breeding or social hunting) to be independent of variation in that domain. For example, signal complexity in nonhunting contact calls or in alarm calls should be unrelated to variation in behavioural coordination related to social hunting. In terms of communicative perception, we would expect the processing of signals and cues to be highly developed in receivers of species whose groups require such coordination, in comparison to receivers of species lacking such coordination. By ‘highly developed’ we mean that receivers will have greater sensitivity to potentially rapid changes in signals or cues, greater acuity in the modality of those signals and cues, and more rapid processing of relevant information gained from others (Stevens, 2013).

To our knowledge, no empirical studies exist that specifically test the behavioural coordination hypothesis with regard to communication. We do know that in strepsirrhine primate species, individuals in species with larger social groups have greater hearing sensitivity and better ability to hear high frequencies than individuals from species with smaller social groups (Ramsier, Cunningham, Finneran, & Dominy, 2012), although it is important to stress that group size is just one proxy for social complexity. These data would be relevant to the behavioural coordination hypothesis if enhanced sensory physiology decreases errors in signal-derived information flow or increases the space over which signals could be detected, or allows for increased crypticity of signals where signal detection by predators, prey or conspecifics is detrimental. Certainly further work is needed on the processing of social information.

Mate Bonding Hypothesis

The ‘mate bonding hypothesis’ is an extension of the ‘Scheherazade hypothesis’ (Dunbar & Shultz, 2017), which addresses sexual selection in species with large brains, such as humans. The idea is that the need to maintain mate fidelity in distant hominid ancestors drove a need for greater cognitive processing ability (Gavrilets, 2012; Miller, 1999). Dunbar and Shultz (2017) note that a more comparative view indicates that establishing and maintaining long-term pair bonds is generally cognitively demanding. This might help explain why long-lived bird species with lifelong pair bonds have larger brains than species that remate every year (Shultz & Dunbar, 2007; West, 2014).

If greater cognitive processing ability in the social domain is needed for the maintenance of long-term pair bonds, we would expect signallers to produce a diversity of signals related specifically to that maintenance. As such, individuals of long-term pair-bonded species should have more complex courtship- and pair bond-related signals in comparison to individuals of species with different mating systems (e.g. siamangs, *Hylobates syndactylus*: Geissmann & Orgeldinger, 2000; rufous-and-white wrens, *Thryothorus rufalbus*: Douglas, Heath, & Mennill, 2012). We would also expect signal complexity to end at that pair bond-related domain for such species, assuming that mate-bonding social coordination does not extend beyond coordination of the association between the mates. Variation in signal complexity in other domains (such as territorial displays, competitive displays or antipredator calls) should be uncorrelated with variation in pair-bondedness. From the standpoint of receivers, we would likewise expect greater sophistication of processing of signals and cues in the context of pair bond maintenance, but not necessarily in other domains such as food finding or predator avoidance.

Machiavellian Intelligence Hypothesis

The ‘Machiavellian intelligence hypothesis’ was the earliest explicit argument about social complexity driving increased social cognition. If individuals benefit from life in social groups, they must act in ways that maintain those groups. However, those same individuals may occasionally benefit from more selfish activities that come at the expense of other group members. For example, an individual that discovers food can signal to attract group members to the benefit of all, but that individual could also withhold signalling such that it alone benefits. Given that social costs of selfishness can accrue through different mechanisms (e.g. tit-for-tat accounting; Krama et al., 2012), balancing individual- and group-level needs is thus thought to be a cognitively demanding problem that individuals in social groups must solve (Byrne & Whiten, 1988; Humphrey, 1976).

Although the Machiavellian intelligence hypothesis originally incorporated cohesive and prosocial behaviour in its framework for social cognition (van Schaik et al., 2012), subsequent theoretical and empirical work heavily emphasized behaviour patterns that were deceptive, exploitative or selfish (Byrne & Whiten, 1988; Whiten & Byrne, 1997). For example, neocortex sizes across nonhuman primate species were found to be associated with rates of tactical deception (Byrne & Corp, 2004). Tactical deception involves the production of signals used in a context different than their normal function and to the producer's advantage (Byrne & Whiten, 1992). A classic example of tactical deception is the deceptive use of an alarm call – i.e. when a predator has not actually been detected – by a signaller that chases competitors away from a limited food source, as seen in tufted capuchins, *Cebus apella nigritus* (Wheeler, 2009).

Under the Machiavellian intelligence hypothesis, signal variation and complexity should differ depending upon whether one considers the cooperative and prosocial side of the possible interactions (see ‘social brain hypothesis’ below) or the deceptive and competitive side (Lucas et al., 2018). Cooperative and prosocial interactions among individuals should entail changes in behaviour induced in the receiver that are advantageous for both receiver and sender. Conversely, deceptive and competitive interactions among individuals should entail changes in behaviour induced in the receiver that are advantageous for the sender but disadvantageous for the receiver. The deceptive and competitive side often results from the use of false signals that effectively parasitize an existing signalling system, where the costs of ignoring such signals by receivers are typically higher than the costs of inappropriately responding to them (Mokkonen & Lindstedt, 2016). As such, signals used in deceptive or competitive interactions should lack diversity and flexibility beyond the use of a signal from one behavioural system or context (e.g. alarm call) for a different context (e.g. exploiting a limited food resource; Lucas et al., 2018). Given the high costs of ignoring an alarm call if it honestly signals a potential predator (a false negative), compared to the costs of responding and losing access to food if a predator is not actually present (a false positive), we would expect little selection pressure on receivers to evolve more sophisticated perceptual abilities, as long as the dishonest use of the signal is relatively rare compared to the honest use of the signal and the cost of false negatives is considerably higher than the cost of false positives. Conversely, if dishonest signalling increases the costs of false positives to receivers sufficiently, we would expect increased selection pressure for more sophisticated perception and cognitive processing to detect deceptive signals and to remember dishonest signallers.

Social Brain Hypothesis

As discussed above, the cooperative and prosocial side of the Machiavellian intelligence hypotheses overlaps substantially with the social brain hypothesis. The social brain hypothesis relates to ‘the need to create functional, cohesive, bonded social groups as a means of solving’ ecological problems (Dunbar & Shultz, 2017, p. 5). Ecological constraints facing a particular social species should serve as strong selection pressures on the size and stability of social groups and so will, in part, affect complexity of those groups (Fig. 1; see also Krause & Ruxton, 2002). As an example from species we have studied, chickadees (genus *Poecile*) and titmice (genus *Baeolophus*) occur regularly over the winter in small and stable flocks of conspecifics, and also regularly flock with each other (Harrap & Quinn, 1995; Smith, 1991). Chickadees, titmice and tits (all members of the Paridae) – and the satellite species that associate with them (Contreras & Sieving, 2011; Farley, Sieving, & Contreras, 2008; Morse, 1970) – benefit from such social groups in terms of territorial defence (Ekman, 1979; Ekman, Cederholm, & Askenmo, 1981), predator avoidance or deterrence (Hetrick & Sieving, 2012; Nolen & Lucas, 2009; Templeton, Greene, & Davis, 2005; Templeton & Greene, 2007) and food finding (Freeberg & Lucas, 2002; Mahurin & Freeberg, 2009; Suzuki & Kutsukake, 2017).

Under the social brain hypothesis, we would expect that the needs of cooperative and prosocial behaviour in chickadee flocks would require considerable diversity and flexibility of signal use, as well as efficient and sensitive perceptual abilities on the part of receivers. These properties require a complex communicative system (Freeberg & Krams, 2015; Sewall, 2015). This expectation is in line with the extraordinarily large and diverse vocal repertoires of parid individuals (Baker & Gammon, 2007; Sturdy, Bloomfield, Charrier, & Lee, 2007). This is especially true of the *chick-a-dee call*, which is used throughout the year in a wide range of contexts related to social cohesion. This call system is one of the few open-ended vocal signals documented outside of human language (Freeberg & Lucas, 2012; Krams, Krama, Freeberg, Kullberg, & Lucas, 2012).

The social brain hypothesis emerges as the clearest single hypothesis predicting a wide range of diverse signals to be used under a wide range of social contexts for species in more complex, as opposed to relatively simple, social groups. In species with relatively complex groups, the greater number of individuals, greater diversity of individuals and/or the greater diversity of relationships among individuals requires greater signalling complexity for effective manipulation of the behaviour of others and more sophisticated perceptual abilities for detecting and processing the signals and cues of others (Freeberg et al., 2012; Peckre et al., 2019; Sewall, 2015). There should be stronger pressure to signal a diversity of messages, including individual and perhaps group identity, behavioural tendencies, affective state, and potentially, regarding external stimuli. Signallers and receivers will often weigh signals and cues differently depending upon their experiences with one another (Bergman & Sheehan, 2013). Individuals in socially complex species should be sensitive to changes in social context, and an individual should be able to adjust its signalling quickly in light of those changes, perhaps by changing signal type or the structuring or ordering of particular signals used (Cheney & Seyfarth, 2018; Coppinger et al., 2017; Zuberbühler, 2008). The social brain hypothesis has considerable support from comparative studies of brain volumes – from analyses of both whole brain and specific brain regions like the neocortex (Dunbar & Shultz, 2017) – although, as mentioned, brain size is not synonymous with social cognition. Importantly, within both humans (Bickart, Wright, Dautoff, Dickerson, & Barrett, 2011; Lewis, Rezaie, Brown, Roberts, & Dunbar, 2011) and macaques (Sallet et al., 2011), individual variation in social network size is positively associated with individual variation in relative size of neural regions involved in social cognition. Surprisingly, however, we know relatively little about correlated patterns in the complexity of communicative systems.

FUTURE CONSIDERATIONS: COMMUNICATION IS ESSENTIAL

We raised four major hypotheses to explain the evolution of social cognition, and for each discussed predictions for communication systems under those hypotheses. Despite the fact that these hypotheses are not mutually exclusive, each hypothesis raises at least one unique prediction about the role of communication in social cognition (Fig. 1). Two hypotheses predict a *reduction* in complexity of signals in certain domains – the behavioural coordination hypothesis and Machiavellian intelligence hypothesis posit high context specificity (and therefore reduced complexity) in domains of coordination and deception, respectively. Two hypotheses predict an increase in perceptual processing abilities in specific domains (the various coordination domains in the behavioural coordination hypothesis and the courtship/pair bond domain for the mate bonding hypothesis). The social brain hypothesis predicts *increased* complexity of signals and a corresponding increase in perceptual processing abilities in a wide range of contexts related to social cohesiveness. We now need to test these predictions in comparative and, hopefully, experimental work.

That such predictions about the role of communication in the evolution of social cognition have rarely been tested is both unfortunate and surprising. As mentioned, the Machiavellian intelligence hypothesis was among the first explicit ‘social intelligence’ hypotheses to be raised. An important volume collected seminal and new theoretical and empirical papers related to this hypothesis three decades ago (Byrne & Whiten, 1988), yet only a few of these papers discussed communication (e.g. Seyfarth & Cheney, 1988). Indeed, our discussion here is framed around an important recent review article (Dunbar & Shultz, 2017) that only alludes to communication quite late in the paper. We hope our article underscores the critical role of communication in social cognition, and so the need for increased study of communication to address questions of the evolution of social cognition.

TWO FINAL THOUGHTS

Communication is Two-sided and Multimodal

A growing body of comparative and experimental work indicates that social complexity can drive signalling complexity (Freeberg et al., 2012; Sewall, 2015). What about the other side of the communicative interaction that we have discussed – that of signal and cue perception? Although this has been much less studied, comparative evidence supports the argument that social complexity drives more sophisticated signal perception (Ramsier et al., 2012). Therefore, we encourage researchers studying both social cognition and communication to start to focus more on the perception of signals and cues by individuals. Signals and cues in socially complex species are conveyed via mixes of different sensory modalities (Peckre et al., 2019). For example, whereas most birds emphasize vocal communication, they also rely on kinesthetic signals and cues (head, body, feather positions and actions) requiring visual perception by receivers. In nonhuman primates, repertoires of both vocal signals and facial expressions can be immensely diverse (Liebal, Waller, Burrows, & Slocombe, 2013). Hence, assessment of variation in signal and cue processing abilities across modalities will be fundamental to testing predictions of the four classes of hypothesis we have raised here.

Consider the assessment of detail related to facial orientation in primate social cognition. The fine musculature of primate faces appears to be more intricate than that of other mammals (Burrows, 2008). This musculature makes possible a greater diversity of facial expressions and flexible variation in those expressions (Dobson, 2012). Moreover, the visual perceptual systems of primates are particularly fine-tuned to such diversity of, and variation in, expressions, with distinct rapid (subcortical) and slower (cortical) perceptual processing subsystems (Burrows, 2008). Individuals of different great ape species react adaptively and flexibly in food choice behaviour depending upon facial expressions of humans with whom they are interacting and who had been manipulating those food items (Buttelmann, Call, & Tomasello, 2009), as well as the eye gaze of human observers (Kaminski, Call, & Tomasello, 2004). Similar sensitivity to human eye gaze in competitive food-obtaining tasks has been documented in rhesus macaques, *Macaca mulatta* (Flombaum & Santos, 2005; Ronald, Fernández-Juricic, & Lucas, 2018). Social complexity has been associated with ability to process important attributes of faces, such as facial orientation and eye gaze. For example, in studies involving a human 'competitor' for perceived access to food, socially complex ring-tailed lemurs, *Lemur catta*, were more sensitive to facial orientation of the human than were less socially complex lemur species (Sandel, MacLean, & Hare, 2011).

Social Entropy and Communication

As we define the term, social entropy is an additional dimension of an individual's social environment that potentially plays a critical role in both social complexity and communicative complexity. For example, individuals living in groups with high social entropy have less ability to predict the nature of each next social interaction (e.g. the individual involved and what the interaction might be) compared to individuals living in groups with low social entropy. Consider an example of low social entropy – the common black hawk, *Buteogallus anthracinus*. The social group in this species is a mated pair, and the pair engages in little social interaction with other conspecifics (Schnell, 1994). The pair coordinates incubation of eggs and young, and possibly territorial and nest defence. Each individual would have relatively little uncertainty about the behavioural tendencies or motivations of the other individual. Conversely, the Harris' hawk, *Parabuteo unicinctus,* is a species in which the social group is made of multiple individuals engaged in cooperative hunting and group breeding (Dwyer & Bednarz, 2011). Multiple individuals even perch together regularly. For an individual Harris' hawk, the next encounter and the next individual to interact with are considerably less predictable than for an individual common black hawk. Communication in both species has not been studied in great detail, but we would predict greater communicative complexity for Harris' hawks compared to common black hawks. The specificity of that complexity (Fig. 1) could help us shed light on the nature and evolution of social cognition in these species.

What ecological conditions generate high or low entropy in social systems? What are the roles of fission–fusion dynamics in social cognition and communication (Aureli et al., 2008)? Under what conditions do we predict increased individual distinctiveness in signal variation (e.g. behavioural coordination hypothesis and social brain hypothesis), and how might that constrain other aspects of communicative complexity? We expect considerable bidirectional influences among the various social factors impacting social cognition and communication (Fig. 1). We have experimental evidence that manipulations of group size (a key metric of social complexity) cause differences in vocal complexity, indicating that social complexity can drive communicative complexity (Freeberg, 2006). Conversely, numerous authors have pointed out that the reverse relationship could hold in many systems, with more complex communicative systems making more complex social structures possible (McComb & Semple, 2005). We believe that increased experimental and comparative work will shed light on the factors driving increases in social cognition, social complexity and communicative complexity. Although cognitive processing in general is not necessarily social, communication is inherently social. Therefore, communication is fundamental to sociality and to social cognition, and so if we hope to increase our understanding of the nature and evolution of social cognition, we need to focus our studies more on communication.

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