

Social Cognition and the Evolution of Language: Constructing Cognitive Phylogenies

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Human language and social cognition are closely linked: advanced social cognition is necessary for children to acquire language, and language allows forms of social understanding (and, more broadly, culture) that would otherwise be impossible. Both “language” and “social cognition” are complex constructs, involving many independent cognitive mechanisms, and the comparative approach provides a powerful route to understanding the evolution of such mechanisms. We provide a broad comparative review of mechanisms underlying social intelligence in vertebrates, with the goal of determining which human mechanisms are broadly shared, which have evolved in parallel in other clades, and which, potentially, are uniquely developed in our species. We emphasize the importance of convergent evolution for testing hypotheses about neural mechanisms and their evolution.

Language and Social Cognition Are Closely Linked

Social cognition encompasses a number of distinctive capacities, including social learning, imitation, gaze following, and theory of mind (TOM). Such mechanisms form core elements of animal social behavior and human imitative culture. Language can be defined as a bidirectional system that permits the expression of arbitrary thoughts as signals and the reverse interpretation of those signals as thoughts. Although most animals have communication systems that allow some biologically important concepts or emotions to be expressed vocally, visually, or otherwise, humans appear to be unique in possessing a system that allows *any* concept we can entertain to be expressed and understood. Yet although language itself is unique to our species, many of the mechanisms underlying it are shared with other species (Fitch, 2010).

Social cognition is closely linked to the evolution of language. Advanced social cognition is required for children to acquire language: sophisticated “mind-reading” abilities are necessary to deduce word meanings and communicate pragmatically (Clark, 1987; Macnamara, 1972). Second, once in place, language provides a powerful new tool for social cognition, one that is at the center of human culture. Our capacity to share thoughts socially allows human cultures to accumulate knowledge in a way that would be impossible without language and underpins the progressive accumulation of complexity seen in most aspects of culture, from science and technology to myth and religion. Together, social cognition and language probably formed an evolutionary cycle wherein advances in one fed advances in the other, and it is unclear what human cognition (social or otherwise) would be like without the powerful cultural augmentation that language provides. Research on nonhuman animals can play a central role in understanding the evolution of social cognition on its own, nonlinguistic, terms.

Multiple Mechanisms Are Needed for Language

Although language appears as a seamless whole, with phonology, syntax, semantics, and pragmatic processes working together, many dissociable mechanisms underlie linguistic

competence. These mechanisms together make up the faculty of language in a broad sense, and most of them exist in some form in other animals. We can roughly classify these mechanisms by whether they involve signaling (e.g., perceptual and motor systems underlying speech and sign), semantics (central cognitive mechanisms supporting concept formation, expression, and interpretation), or syntax (structure-generating mechanisms that map between signals and concepts). Both signals and semantics have a strong social component. Signals used in linguistic communication, whether spoken, signed, or written, must be learned and shared among the members of a linguistic community, and this shared lexicon requires sophisticated imitation of complex signals. Semantic interpretation requires an ability to infer the intentions of a signaler based on rather indirect cues (such as gaze direction). When a child hears the word “rabbit” spoken, a huge number of possible meanings might be inferred (e.g., “cute,” “furry,” “hopping,” “dinner”). Despite this complexity (Macnamara, 1972; Quine, 1970), children typically hone in unerringly on the intended meaning of a speaker by relying on conceptual constraints on possible word meanings (Clark, 1987; Markman, 1990). Many of these constraints are shared with other species, suggesting that a rich set of conceptual building blocks was already in place before language evolution began (Cheney and Seyfarth, 2007; Kaminski et al., 2004; Seyfarth and Cheney, 2005).

Finally, human language rests upon a rich pragmatic basis (Grice, 1975), including a strong motivation to share novel information with others. This drive to share meaning seems so natural to us that it has taken many years to realize that it is very unusual among animals, with the closest parallel perhaps being the honeybee dance “language” (Hockett, 1960; Lindauer, 1971). But the drive to share *novel* information requires a signaler to know what the intended recipient does and does not know (TOM). Nonhuman primates generally fail to take receiver’s knowledge into account when signaling (e.g., Cheney and Seyfarth, 1980; Rendall et al., 2000), suggesting that TOM, to the extent that it is present at all, is not employed pragmatically

in communication. In summary, social mechanisms needed for language acquisition include a capacity for imitation for the signaling component, and mind-reading and TOM for the semantic and pragmatic components. Numerous studies in animal cognition provide insight into the evolution of these mechanisms.

Building Cognitive Phylogenies: Homology and Convergence

Researchers in comparative cognition study multiple species, seeking to uncover similarities and differences in each of these cognitive mechanisms, studied at multiple levels of description, including the genetic, neural, and behavioral levels. Such similarities allow us to generate and test hypotheses about the evolution of cognition. Two broad kinds of similarities need to be distinguished, termed “homology” and “analogy,” both of which play important roles in cognitive phylogenetics.

Homologous mechanisms (homologs) are shared by descent from a common ancestor that possessed the mechanism. For example, the differences in imitation abilities between apes and monkeys have been used to infer that the last common ancestor (LCA) of humans and great apes had well-developed imitation capacities, while the LCA of apes and monkeys did not. Similarly, the existence of trichromatic color vision in Old World monkeys, apes, and humans indicates that trichromacy evolved in the LCA of all catarrhines (Jacobs, 1996). Nonhuman primates have traditionally been the focus of comparative research on social cognition, typically by researchers seeking homologs of human mechanisms in order to infer the capabilities of our extinct ancestors.

Recently, comparative research on social cognition has broadened considerably to include nonprimate mammals (dogs, rats, goats), many bird species (especially among *corvids*: jays, crows, ravens, and their relatives), reptiles, fish, and social insects (Table 1). Results of this work have often seemed surprising, revealing cognitive abilities in dogs or ravens that are lacking in our closer primate relatives. But surprise at such results is unwarranted, reflecting an outmoded “scala naturae” view of evolution in which cognitive capacities increase with a species’ relatedness to humans (Striedter, 2004). From a modern Darwinian viewpoint, we instead expect a species’ cognitive abilities to evolve to fit its “cognitive niche.” For example, we expect species relying on complex navigation to evolve excellent spatial memory, and species living in complex social environments to exhibit superior social cognition. This perspective leads us to expect convergent evolution of analogous cognitive mechanisms (analogs) in widely separated species that face similar cognitive problems.

Evolutionary Hypotheses Can Be Tested Using Convergence

The “social intelligence hypothesis” is a leading contemporary hypothesis that attempts to explain the evolution of intelligence, in general, as a result of selection for social intelligence in particular (Byrne, 1997; Dunbar, 2003; Humphrey, 1976; Jolly, 1966). It follows from the simple fact that the most cognitively challenging entities most organisms must cope with are other animals, often conspecifics. This hypothesis contrasts with the older “physical intelligence hypothesis” that supposes that intelligence, particularly human intelligence, is the result of

intense selection for the use of tools and other manipulations of the environment.

Crucially, such contrasting hypotheses can be tested using convergent evolution. Because analogs reflect independent evolutionary events, they constitute statistically independent samples that can support rigorous testing of evolutionary hypotheses. In contrast, homologous mechanisms by definition evolved once, and their presence in multiple descendent species constitutes only a single data point. The 4000 or so passerine birds with vocal learning represent but a single evolutionary event. It is important to recognize, however, that convergent evolution can occur in homologous substrates. For example, hippocampal enlargement has apparently evolved repeatedly in different species of food-caching birds. Although the hippocampus itself is a homolog in these species, the episodes of enlargement are convergent and represent independent events. Furthermore, capabilities that are convergent at one level (e.g., behavioral) may employ mechanisms that are homologous at another level (e.g., genetic). The use of the same genes in the specification of convergently evolved traits appears to be surprisingly common in development, and we can expect many examples in the cognitive realm (Fitch, 2009b). Thus, whether a given cognitive mechanism is homologous or convergent in a phylogenetic analysis depends on the hypothesis being tested and the level of analysis.

In this paper, we review comparative research on social cognition, aiming to build tentative cognitive phylogenies of the mechanisms underlying social intelligence, and to test evolutionary hypotheses concerning such mechanisms. This broad comparative approach, which we call “cognitive phylogenetics,” has substantial promise to fuel our understanding of the evolution and neural basis of both human language and culture, and social cognition more generally. Although current data remain too incomplete to support definitive conclusions, they point to gaps in our present knowledge, and allow us to reject some long-standing assumptions about animal social cognition. Finally, we discuss the implications of empirical data from animals for hypotheses about language evolution.

Social Cognition Involves Multiple Mechanisms

Social cognition involves a set of interacting but separable mechanisms, and the recent literature has led to an extensive dissection of social cognition and a correspondingly daunting profusion of terms. In this section, we discuss two sets of mechanisms: the use of gaze direction to infer another’s focus of attention, and of TOM, in which one organism represents what another one does or doesn’t know.

Gaze Detection Is Shared Widely among Vertebrates, whereas Geometric Gaze Following May Be Restricted to a Few Species

For humans, monitoring others’ head and eye orientation (gaze) is a central feature of social life and communication (Brooks and Meltzoff, 2002), even influencing eye anatomy (Kobayashi and Kohshima, 2001). Newborn humans are already responsive to their mothers’ visual orientation (Farroni et al., 2002), and coordination with others’ head and eye orientation to look in the same direction (gaze following) or at a specific target (joint visual attention) develops during early ontogeny (Butterworth

Table 1. Species and Clades Studied in Contemporary Social Cognition Research

	Common Name	Genus	Species	Major Clade	Minor Clade
Vertebrates	Common Marmoset	<i>Callithrix</i>	<i>jacchus</i>	class Mammalia	order Primates
	Chimpanzee	<i>Pan</i>	<i>troglodytes</i>	" "	" "
	Orangutan	<i>Pongo</i>	<i>pygmaeus</i>	" "	" "
	Capuchin	<i>Cebus</i>	<i>apella</i>	" "	" "
	Rhesus Macaque	<i>Macaca</i>	<i>mulatta</i>	" "	" "
	Bottlenose Dolphins	<i>Tursiops</i>	<i>truncatus</i>	" "	order Cetacea
	Humpback Whale	<i>Megaptera</i>	<i>novaeangliae</i>	" "	" "
	Harbor Seal	<i>Phoca</i>	<i>vitulina</i>	" "	suborder Pinnipedia
	S. African Fur Seal	<i>Arctocephalus</i>	<i>pusillus</i>	" "	" "
	Domestic Dog	<i>Canis</i>	<i>familiaris</i>	" "	order Carnivora
	Domestic Goat	<i>Capra</i>	<i>hircus</i>	" "	order Artiodactyla
	Greater Sac-Winged Bat	<i>Saccopteryx</i>	<i>bilineata</i>	" "	order Chiroptera
	Japanese Quail	<i>Coturnix</i>	<i>japonica</i>	class Aves	order Galliformes
	Pigeon	<i>Columba</i>	<i>livia</i>	" "	order Columbiformes
	Bald Ibis	<i>Geronticus</i>	<i>eremita</i>	" "	order Threskiornithidae
	Budgerigar	<i>Melopsittacus</i>	<i>undulatus</i>	" "	order Psittaciformes
	Kea	<i>Nestor</i>	<i>notabilis</i>	" "	" "
	African Gray Parrot	<i>Psittacus</i>	<i>erithacus</i>	" "	" "
	European Starling	<i>Sturnus</i>	<i>vulgaris</i>	" "	order Passeriformes
	Woodpecker Finch	<i>Cactospiza</i>	<i>pallida</i>	" "	" "
Swamp Sparrow	<i>Melospiza</i>	<i>georgiana</i>	" "	" "	
Zebra Finch	<i>Taeniopygia</i>	<i>guttata</i>	" "	" "	
Bengalese Finch	<i>Lonchura</i>	<i>striata domestica</i>	" "	" "	
New Caledonian Crow	<i>Corvus</i>	<i>moneduloides</i>	" "	family Corvidae	
Raven	<i>Corvus</i>	<i>corax</i>	" "	" "	
Rook	<i>Corvus</i>	<i>frugilegus</i>	" "	" "	
Scrub Jay	<i>Aphelocoma</i>	<i>californica</i>	" "	" "	
Archerfish	<i>Toxotes</i>	<i>chatareus</i>	infraclass Teleostei	family Toxotidae	
Red-footed Tortoise	<i>Geochelone</i>	<i>carbonaria</i>	class Reptilia	family Testudinae	
Nonvertebrates	Octopus	<i>Octopus</i>	<i>vulgaris</i>	phylum Mollusca	class Cephalopoda
	Honeybee	<i>Apis</i>	<i>mellifera</i>	class Insecta	order Hymenoptera

This table provides taxonomic information regarding the species discussed in this review. Only the common name is used in the main text. The major and minor clades help to contextualize the phylogenetic position of these species utilizing traditional Linnaean classifications, even when (as for class "Reptilia") this traditional grouping is polyphyletic.

and Jarrett, 1991; Johnson et al., 1998; Moll and Tomasello, 2004). These capacities undergird word learning via joint attention, and are considered a crucial step toward an understanding of mental states like attention and intention (Baron-Cohen, 1995; Tomasello et al., 2005). Gaze processing is a central aspect of human social intelligence. Unlike pointing (which has received much attention in the primate-centered literature), directed gaze is possible for virtually any vertebrate.

Long underestimated, the importance of gaze for nonhuman animals is receiving increased interest (reviewed in Gómez, 2005). Different levels of gaze responsiveness may be distinguished in animals (Figure 1, cf. Povinelli and Eddy, 1996; Schloegl et al., 2007). The most basic level concerns simple detection of others' gaze direction, particularly the awareness that one is being looked at. Gaze detection seems to be based on relatively simple mechanisms (Baron-Cohen, 1995; Povinelli

et al., 1999) that are phylogenetically widespread (reviewed in Emery, 2000), presumably because of their relevance to social or antipredator behavior.

A second level of gaze responsiveness concerns the following of others' gaze direction. Originally described in primates (Povinelli and Eddy, 1996a; Tomasello et al., 1998), gaze following has now been demonstrated in distantly related mammals (dogs, Miklósi et al., 1998; goats, Kaminski et al., 2005) and birds (ravens, Bugnyar et al., 2004; rooks, Schloegl et al., 2008a; and bald ibises, Loretto et al., 2010). Like gaze detection, gaze following may be based on a relatively simple mechanism (Povinelli and Eddy, 1996a): a socially triggered orientation response may result in subjects aligning their view with that of another individual gazing toward something, allowing them to search for something of interest themselves. While this explanation may account for following gaze into distant space, it does not explain

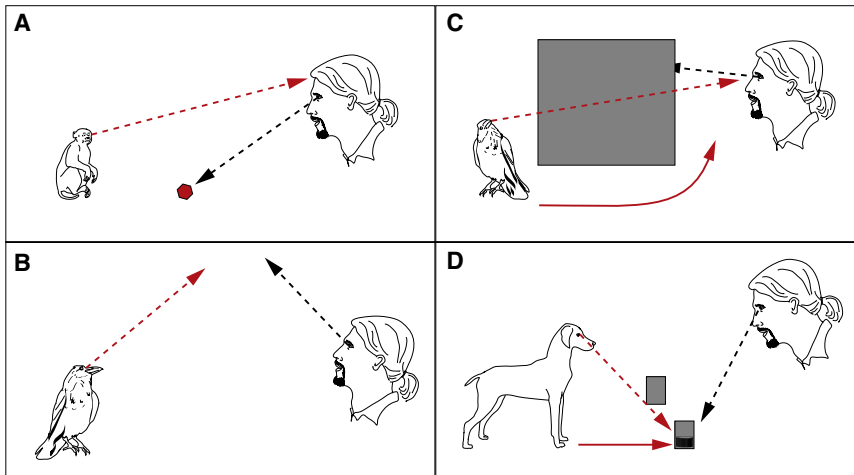


Figure 1. Different Levels of Gaze Responsiveness

(A) A macaque monkey is aware that a human experimenter looks in its direction and thus refrains from taking the food.

(B) A raven follows the gaze direction of a human experimenter above its head, i.e. it looks up.

(C) A raven also follows the gaze of a human experimenter behind a visual barrier by relocating its position.

(D) A dog uses the gaze direction of a human experimenter to find food hidden under one of two inverted cups. Dotted arrows indicate gaze direction. Full arrows indicate movement of test subjects.

instances in which subjects track others' gaze direction geometrically behind visual barriers (geometrical gaze following; Tomasello et al., 1999). Simply looking for something of interest in the direction of the others' gaze would result in subjects searching in front of the barrier, but if they reposition themselves to look behind a barrier, it suggests they appreciate the difference between their own and another's line of sight (Povinelli and Eddy, 1996a). This ability has only been demonstrated in great apes (Bräuer et al., 2005) and two corvid species (Schloegl et al., 2008a). Geometrical gaze following is thought to rest on a cognitively more sophisticated mechanism; developmental data from ravens indicate that geometrical gaze following develops later and shows a different habituation pattern than gaze following into space (Schloegl et al., 2007).

A third level of gaze responsiveness is the ability to identify the others' target of attention, i.e., what others are looking at. Most nonhuman species, including apes, monkeys, and ravens, find it surprisingly difficult to use the gaze direction of a human experimenter, or a conspecific, as a cue to find hidden food (Anderson et al., 1996; Call et al., 2000; Schloegl et al., 2008b). Methodological changes (e.g., combination of gaze with other cues) and experience with human communicative gestures can improve performance in various species (chimpanzees, Barth et al., 2005; capuchins, Vick and Anderson, 2000; ravens, Schloegl et al., 2008c; dolphins, Pack and Herman, 2004; and fur seals, Scheumann and Call, 2004). Dogs, however, are outstanding in solving these tasks instantly and reliably across a large number of variations (Agnetta et al., 2000; Miklósi et al., 1998, 2004), and although they have not been tested formally for geometrical gaze following, they seem to understand how barriers impair others' perception (Bräuer et al., 2006). Why do dogs outperform primates in such tasks? One explanation may be that, during domestication, dogs have been specifically selected to attend to human communicative cues (Hare et al., 2002; Miklósi et al., 2003). Most other species seem to have problems in understanding the cooperative, communicative nature of the task, or they may be biased by competitive motives (Hare and Tomasello, 2004). Competitive species like chimpanzees and ravens may thus find it difficult to develop certain gaze following skills, without this indicating a lack of mentalistic understanding (Gómez, 2005).

Taken together, comparative evidence from human children, nonhuman primates, other mammals, birds, reptiles, and fish suggests that gaze responsiveness is widespread among vertebrates. In contrast, gaze following requires active use of others' gaze cues, and to date only five groups of mammals and three groups of birds are known to follow gaze. Simple mechanisms may account for tracking others' gaze into distant space, whereas more sophisticated mechanisms are required for geometrical gaze tracking, which has only been demonstrated in a handful of primate and corvid species. Most nonhuman species have problems in identifying the target of others' gaze. Surprisingly, dogs provide the best-attested exception, perhaps due to their high level of cooperativeness. How much ape or corvid failures depend on cognitive limitations, or cooperative versus competitive motivations, remains an open question. These data demonstrate the separability of gaze processing into multiple distinct mechanisms, perfect for building a cognitive phylogeny (see Discussion subsection).

Nonhuman Animals Show Some of the Skills underlying TOM

TOM is a core human capacity, underlying many pragmatic aspects of adult language use and closely tied to child language acquisition (de Villiers and Pyers, 2002). Since Premack and Woodruff's (Premack and Woodruff, 1978) seminal paper asked "Does the chimpanzee have a theory of mind?", the question of whether or not precursors of TOM can be found in nonhuman primates has been a core controversy (e.g., Povinelli and Vonk, 2003; Tomasello et al., 2003). For years, tests based on cooperative paradigms, in which subjects must rely on help from knowledgeable human experimenters, provided little evidence of TOM in chimpanzees (Povinelli and Eddy, 1996; Povinelli et al., 1990; Premack and Woodruff, 1978). More recent competitive designs (Figure 2), in which subjects compete with conspecifics and/or human experimenters for access to food (Hare et al., 2000), have led to unexpectedly strong results, probably because they are ecologically more meaningful to primates (Hare, 2001). Chimpanzees can differentiate between individuals that can and cannot see food behind a barrier (Bräuer et al., 2007; Hare et al., 2000; but see Karin-D'Arcy and Povinelli, 2002), and those that have and have not seen the hiding of food in the recent past

(Hare et al., 2001; Kaminski et al., 2008). Although mixed results have been reported for some monkeys (brown capuchins, Hare et al., 2003; Kuroshima et al., 2002, 2003; common marmosets, Burkart and Heschl, 2007), rhesus macaques have been shown to discriminate between human experimenters who can and cannot see food (Flombaum and Santos, 2005), as well as individuals who can and cannot hear the removal of food (Santos et al., 2006), indicating multimodal sensitivity to others' perception (but see chimpanzees; Bräuer et al., 2008). These data suggest that subjects can distinguish between conspecifics who *know* where food is hidden from "guessers" who know that food has been hidden, but don't know where. This "knower/guesser" distinction may require the subject to represent, in some form, the mental awareness of others: a basic form of TOM.

Outside primates, the strongest evidence of mechanisms involved in TOM comes from corvids tested with variants of the competitive food retrieval design, involving the caching and pilfering of food (Clayton et al., 2007). Both scrub jays and ravens differentiate between competitors that have or have not seen food cached in particular locations, selectively recovered food whose caching was observed (Bugnyar and Heinrich, 2005; Emery and Clayton, 2001), altered their cache protection strategies (Dally et al., 2005, 2006) and, when tested as bystanders, adjusted their pilfering strategies (Bugnyar and Heinrich, 2005, 2006). Scrub jays also differentiate between conspecifics that can and cannot *hear* caches being made (Stulp et al., 2009), suggesting that, as in macaques, they can also use this knowledge in the auditory domain.

Thus, some primates and corvids are capable of solving "knower-guesser" tasks: they can take others' perception into account and draw inferences about the probability of winning food from, or losing it to, those others. These findings jibe with results from geometrical gaze following (Bugnyar et al., 2004; Tomasello et al., 1999) and support the hypothesis that the poor performance of nonhuman primates on cooperative tasks may better reflect their competitive motivation than their cognitive abilities per se (Gómez, 2005; Hare and Tomasello, 2004).

Little agreement exists regarding whether these results can be interpreted as evidence for mental state attribution and basic TOM in nonhuman animals (cf. Povinelli and Vonk, 2003; Tomasello et al., 2003). Indeed in most, if not all, studies, subjects had to integrate observable features from the others' current and past behaviors, and might have based their decisions solely on their *own* rather than the others' perspective (Heyes, 1998; Perner, 2010; Povinelli and Giambrone, 1999). For instance, subjects might have picked up on perceptual features during the experiment and, by integrating this information with their knowledge about others' behavior in competition for food or food caches, acted according to nonmentalistic rules like "do not go after food if a dominant has oriented toward it" or "recache food in a site that is different from the one where it was cached when the competitor was present" (Penn and Povinelli, 2007). Such heuristics do not require representations of others' mental states, like "know" or "see."

Experience with others' behavior not only improves the subjects' performance but may be a necessary precondition for these types of social problem solving skills. Among apes, individuals with different raising conditions (enculturated versus

nonenculturated apes; Call and Tomasello, 2008) show different social capacities. Scrub jays with pilfering experience show recaching when observed, while birds without experience as thieves do not (Emery and Clayton, 2001). Similarly, ravens with appropriate experience distinguish between efficient and inefficient human pilferers (Bugnyar et al., 2007). Thus, experience plays an important role in developing social intelligence. However, there is good reason to doubt that primates and corvids apply simple associatively learned rules of thumb in knower-guesser experiments. First, a variety of surface behavioral cues potentially given by conspecifics during tests hardly affect subjects' performance (Dally et al., 2006; Hare et al., 2000; Kaminski et al., 2008). When subjects were required to distinguish between others solely on the basis of surface behavioral cues in experimental settings, it took them relatively long to do so (if they succeeded at all), and they did not flexibly apply these learned contingencies in novel situations (Call and Tomasello, 2008; Schloegl et al., 2008b).

Therefore, it has been argued that some nonhuman animals are capable of attributing certain mental states (Call and Tomasello, 2008; Clayton et al., 2007). Primates in particular may cope with others' intentions and goals, but not with false beliefs like humans (Call and Tomasello, 2008). Although the capacity to understand false beliefs among humans has long been thought to emerge after age four (de Villiers and Pyers, 2002; Happé, 1995), recent findings suggest that human sensitivity to others' perceptual and knowledge states emerge earlier in ontogeny (reviewed in Caron, 2009). Together with the possibility of TOM in nonhuman primates, this has tempted some authors to propose that mind-reading abilities may be part of an ancient core knowledge system for representing basic domains of cognition (Spelke and Kinzler, 2007). Given the limitations of the comparative data, this interpretation seems premature. Furthermore, even if one accepts the idea of precursor elements of a TOM in some nonhuman primates, striking differences exist from the human system of understanding mental states and intentional agency (Csibra and Gergely, 2006, 2009; Tomasello et al., 2005), especially in their use of such understanding in communication (Seyfarth and Cheney, 2005). How do birds fit into the picture? Given their phylogenetic distance from mammals, it seems unlikely that their mind-reading skills are homologous with those of nonhuman primates. More likely, they constitute analog mechanisms, derived through convergent evolution (Emery and Clayton, 2004), possibly as a result of similar selection pressures. Studies of avian cognition thus offer an excellent opportunity to better understand how and why advanced social cognitive abilities, including those related to TOM, can evolve (see Discussion subsection).

Social Learning, Imitation, and Animal "Culture"

"Cultural" phenomena are of considerable theoretical significance for evolutionary biology, because they offer a system of inheritance and adaptation, much more rapid than genetic transmission processes, and the prospect of a secondary form of behavioral evolution at the cultural level (Laland and Galef, 2009). Studies of such processes in nonhuman animals are of central importance in identifying the roots of the cultural processes that are so distinctive in humans.

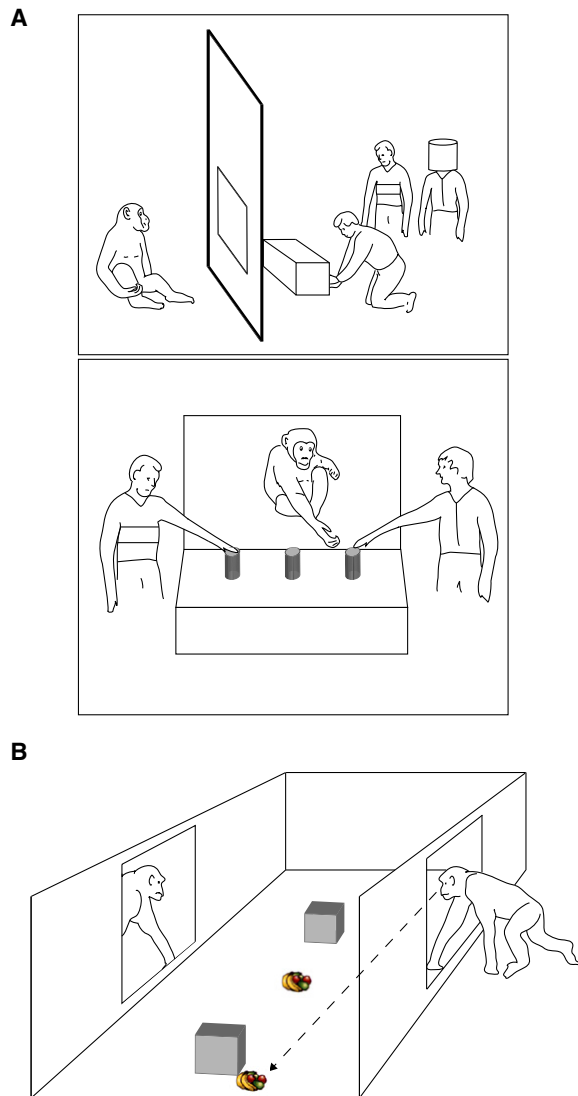


Figure 2. Cooperative versus Competitive Set-Up in Knower-Guesser Experiments

(A) A chimpanzee sees a human experimenter hiding food while two other humans are present, one actively watching the baiting process, the other one having a bucket on his head. In the subsequent test, both humans offer their help to the chimpanzee by pointing toward a particular container. In such a cooperative set-up, chimpanzees must learn, slowly, to prefer the knowledgeable human who had seen the caching over the guesser whose view was blocked by the bucket.

(B) A subordinate chimpanzee (on the right) has the choice to retrieve food that is within view of a dominant conspecific (on the left) or hidden behind a visual barrier. In this competitive set-up, chimpanzees instantly go for the food that cannot be seen by the dominant animal.

A crucial property of culture is that it can give rise to a new level of evolution, cultural evolution, in which traditions diversify progressively in ways analogous to Darwinian biogenetic evolution (Darwin, 1859; Dawkins, 1976; Mesoudi et al., 2004). Language provides a particularly rich example of such cultural evolution via historical change, sometimes termed “glossogeny” (Fitch, 2008; Hurford, 1990), and linguistic elements such as words or grammatical rules can be analyzed using many of the

tools of molecular phylogenetics (Cavalli-Sforza et al., 1992; Lieberman et al., 2007; Pagel et al., 2007). At the heart of culture is a means of high-accuracy copying, which provides the analog of genetic transmission. Human cultural evolution also allows for accumulation of good ideas, a fact that is central to human cultural progress (Tomasello, 1999). There is considerable debate about whether any animal species is capable of imitation of a high enough fidelity to allow such cumulative change (cf. Heyes, 2009; Huber et al., 2009; Tennie et al., 2009; Whiten et al., 2009), and while cultural variants are well documented, (e.g., birds, Lachlan, 1999; Slater and Ince, 1979; and great apes, van Schaik et al., 2003; Whiten et al., 1999), the existence of cumulative culture remains highly contentious.

The Roots of Social Learning May Be Ancient

The relation between social learning and culture is particularly interesting. The last 2 decades have seen an explosion of research investigating the role of social interactions in the development of animal behavior. Recent empirical evidence documents social influences on food choice, tool use, patterns of movement, predator avoidance, mate choice, and courtship (Galef and Laland, 2005). Much has been discovered about the evolutionary roots of social learning and traditions through comparative studies (Fragaszy and Perry, 2003), especially in fish, birds, and nonprimate mammals (Laland and Galef, 2009), as well as insects (Leadbeater and Chittka, 2007).

There is evidence that group-living mammals (Heyes and Galef, 1996), birds (Zentall, 2004), fish (Schuster et al., 2006), and insects (Leadbeater and Chittka, 2007) can learn socially. However, little is known about the evolutionary origins of this ability. An often implicit assumption is that living in social groups favors the evolution of social learning, leading to the idea that social learning is an adaptation for social living. Social learning is a core element of the social intelligence hypothesis (Dunbar and Shultz, 2007; Humphrey, 1976), which suggests that the physical environment does not present the kind of challenges that lead to the evolution of a flexible, intelligent mind, but that the social environment does. This hypothesis predicts relatively limited intelligence in nonsocial animals. But investigation of observational learning in nonsocial animals, such as solitary octopuses (Fiorito and Scotto, 1992) and solitary tortoises (Wilkinson et al., 2010), suggests otherwise: the latter can learn to solve a detour task by observing the actions of a conspecific. Other than these studies, this obvious route to testing the social intelligence hypothesis in nonsocial species remains sadly unexplored.

Vocal Imitation Provides a Form of Cultural Transmission

Despite many examples of animal learning in the visual/motor modalities, the best-studied examples of social learning come from the auditory/vocal domain. A distinction is often made between “motor” imitation and “vocal” imitation, and research and debate on animal social learning has often focused solely on the former (cf. Laland and Janik, 2006). However, vocal production is also a complex motor behavior, and vocal imitation is rendered more challenging by the fact that the movements are mostly invisible and must be inferred from the sounds produced. Despite these difficulties, complex vocal learning has evolved repeatedly in nonhuman animals, and vocal imitation currently

provides our clearest examples of animal “culture.” Darwin considered birdsong the best known analog to human spoken language (Darwin, 1871). Since then, numerous further species capable of vocal learning have been discovered.

One well-studied example of cultural transmission of complex vocal patterns is provided by baleen whale song, especially that of the humpback whale. Humpback males sing long, complex songs during the mating season that are thought both to repel rival males and attract females. At a given time, all of the males in a given area sing the same song, but this song typically changes gradually throughout the mating season (Payne et al., 1983) with complete song replacement in about 15 years (Payne and Payne, 1985). Such replacement cannot be explained by genetic change or male replacement, and thus provides a clear example of a culturally shared and ever-changing vocal repertoire. Under certain special circumstances, local dialects can change much more rapidly. Such an abrupt change was recently documented off eastern Australia, when the population rapidly adopted a novel song apparently carried by just a few males from the west coast population (Noad et al., 2000). Although the functional significance of these changes remains unknown, the results suggest that some preference for novelty may drive the cultural evolution of whale song.

Although Darwin knew that many songbirds must be exposed to conspecific song in order to sing properly themselves, it wasn't until the 1960s that scientists began a detailed investigation of their vocal learning ability (Marler and Tamura, 1964). Marler has memorably dubbed the songbird's need for external input, and the propensity to internalize it, an “instinct to learn” song. Birdsong learning provides an excellent analog for human speech and music learning (e.g., Marler, 2000), convergently evolved and lacking the complexities of semantic meaning that human language entails. Today, birdsong is the best available model system for understanding the neural and genetic bases of a culturally transmitted signaling system (cf. Catchpole and Slater, 2008; Marler and Slabbekoorn, 2004).

The “innate versus learned” dichotomy is inapplicable to birdsong, which is a complex acquired behavior depending upon an innate learning system that filters and guides learning, much like human language. Although the capacity for vocal learning itself is innate (and only present in roughly half of bird species), song learning requires both rich input from the environment and a prolonged period of practice via vocal play. This learning process is shaped by inborn constraints: birds seem to possess an innate filter that allows them to ignore the songs of most species and attend preferentially to conspecific song.

Again like language, the songbird's instinct to learn is fundamentally social: in the natural environment singing adults must be available if the young bird is to sing properly. Although some bird species will learn a song from recordings when isolated (e.g., Marler, 1970), others will not, and young males in many species learn preferentially from a living “tutor” bird (Baptista and Petrinovich, 1986; Immelman, 1969; Mann and Slater, 1995). Finally, although adult males sometimes sing when alone (e.g., in territory defense), courtship song when a female is present is typically more intense and can invoke different patterns of brain activity and gene expression (Jarvis et al., 1998).

Babbling and Subsong

Another apparently fundamental similarity between birdsong and human speech is the need for a period of vocal play early in life, during which an individual vocalizes quietly to itself. This stage, termed “babbling” in speech and “subsong” in birds, appears to be necessary for adequate vocal learning (Catchpole and Slater, 2008; Locke and Pearson, 1990).

The process of song learning varies considerably among species. An important distinction is made between open- and close-ended learners. The former group, exemplified by canaries, retains an ability to learn new songs throughout life. The discovery that this open-ended learning results from neurogenesis in the song nuclei of adult canaries prompted the rediscovery of mammalian neurogenesis, leading to the explosion of research on this topic today (Nottebohm, 2006). In contrast, close-ended or age-limited learners (e.g., zebra finches or white-crowned sparrows) pass through a “sensitive period” during which they memorize one or more songs, storing templates that they later match. After “song crystallization,” the song stays fixed for the rest of the bird's life.

Vocal play has been hypothesized to allow the bird to tune its motor output to auditory input (Marler and Peters, 1982), allowing each individual to adjust to the variation in syrinx structure. This hypothesis should, in principle, apply to individuals of any vocal learning species, since the individual vocal apparatus must always vary to some degree. These observations suggest that other vocal learning species should also go through a stage of vocal play during ontogeny (Fitch, 2006).

Evidence for a “Cultural Ratchet Effect” in Songbirds

A crucial aspect of human culture, sometimes said to be uniquely human, is the cultural ratchet effect: the accumulation of beneficial knowledge and practices. While birdsong provides a nice example of “culture” in the simple sense of cultural transmission of learned features, this is not necessarily directional. Indeed, in many cases, the existence of local birdsong “dialects” is best explained by simple copying errors (Catchpole and Slater, 2008). Copying errors might lead to local divergence, akin to random drift in genetics, without any directional change or improvement being implied (cf. Lynch and Baker, 1994).

Nonetheless, the best known example of a directional cultural ratchet effect in animals comes from research with zebra finches (Figure 3, Fehér et al., 2009). Because songbirds require exposure to conspecific song to sing normally, birds raised in isolation typically produce a rough, relatively structureless song as adults. Fehér and colleagues introduced such isolate male birds into social groups, where young males were exposed only to isolates' poor-quality song. The song of the first-generation birds differed from that of the tutors, in the direction of typical wild-type song. This process was then repeated, with first-generation birds raising and tutoring a second generation and so on. Within three to four generations, these isolate lines produced something approaching normal song. Thus, simply passing through the filtering process of individual ontogeny over multiple generations is apparently enough to sculpt depauperate raw material into species-typical form.

This process has an interesting parallel in human language (cf. Fitch, 2009a). Humans raised in total isolation from language will not invent a normal language themselves (Blumenthal, 2003;

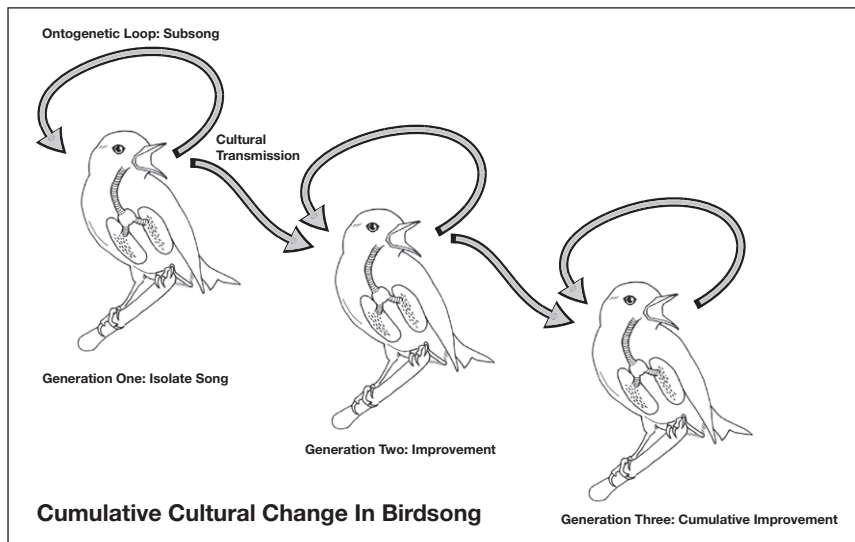


Figure 3. Cumulative Cultural Change in Birdsong

The best examples of cumulative cultural change in nonhuman animals come from birdsong. An isolated male songbird, deprived of song input during the critical period, will produce an aberrant "isolate" song. However, if this aberrant song is provided to a second generation of young males, they will learn it and improve upon it, bringing it closer to the wild-type. Repeating this process over generations leads to a song little different from normal wild-type song.

on the environment, which may facilitate performance by the observer (observational conditioning, emulation, and affordance learning). Finally, observers may learn some part of a demonstrated behavior by either copying it blindly (mimicry), or by understanding the goals and intentions of the model (imitation). Imitation in

Curtis, 1977). In the case of deaf children raised in hearing families, it is common to see "home sign" systems develop, which support basic communicative needs but have nothing like the rich vocabulary and syntax of real signed languages (Goldin-Meadow and Mylander, 1998). However, when many children were brought together in a school for the deaf in Nicaragua, a few "generations" of deaf students developed their own new signed language with a rich lexicon and complex grammar (Senghas et al., 2005). This has parallels in the process by which depauperate pidgin languages, historically used for crude communication in adult trading or slave communities, have developed in a few generations into creoles (such as Tok Pisin or Papiamentu): full languages with a rich, complex linguistic structure (Mühlhäusler, 1997).

Nonvocal Social Information Transmission Is Possible with Multiple Learning Mechanisms

Comparative psychologists have focused on mechanisms that control learning through observation and on their contribution to the transmission of innovations. Highly controlled experiments have been conducted with a wide range of species, investigating what exactly is copied, and what information about the observed action the observer uses (Heyes, 1994; Whiten and Ham, 1992; Whiten et al., 2004; Zentall, 2004, 2006). Animals behave like others for various different reasons. They may simply be predisposed to engage in certain behaviors when others are seen engaging in those behaviors (species-typical behaviors). Being in the presence of conspecifics may result in increased general arousal, which makes certain behaviors more probable (motivational effects). The behavior of others may draw attention to a place or object independently of the behavior itself, and that attention may facilitate learning (perceptual enhancement effects). Such learning may be merely socially biased (Fragaszy and Visalberghi, 2004) by, for example, following one's mother and developing preferences for certain routes or food trees (Schiel and Huber, 2006), followed by individual learning there. Observers may also learn the effect of the observed behavior

this sense is an important neurocognitive process that bridges the gap between one mind and another, powering cognitive and social development in infancy and childhood, promoting empathy and cooperation in our relationships with others, and providing a distinctively human channel of cultural inheritance (Heyes, 2009).

Imitation Research Has Addressed Two Distinct Problems

Imitation research traditionally focuses on two distinct problems. The correspondence problem, favored by cognitive neuroscientists, asks how is it possible for actions as seen to be matched with actions as imitated. The transfer of skill problem, favored by ethologists and comparative psychologists, asks how complex behaviors can be acquired by observation. Most scholars agree that when an individual replicates an action it observes being performed by another individual, a matching system is required to allow conversion of observed actions into actions executed by oneself. In other words, visual input needs to be transformed into corresponding motor output. The same principle holds for the auditory modality, e.g., in song learning.

Most neurocognitive models of imitation require that observers possess a motor representation of the demonstrated action before they observe it being performed (cf. Hurley and Chater, 2005). But, if the essence of imitation lies in the activation of responses already in the repertoire of the observer, how are *new* skills acquired? Imitative learning in the sense of the acquisition of new skills by observation must therefore be distinguished from response facilitation, priming, stimulus enhancement, and other forms of perception-motor coupling, or many other forms of social influences.

Imitation Allows the Cultural Transmission of Information

It has been clear for more than a century that imitation provides a nongenetic route for the inheritance of phenotypic attributes and has the potential to support culture. The issues that remain unclear concern the type of imitation that has this potential, and its importance, relative to other cognitive and social attributes,

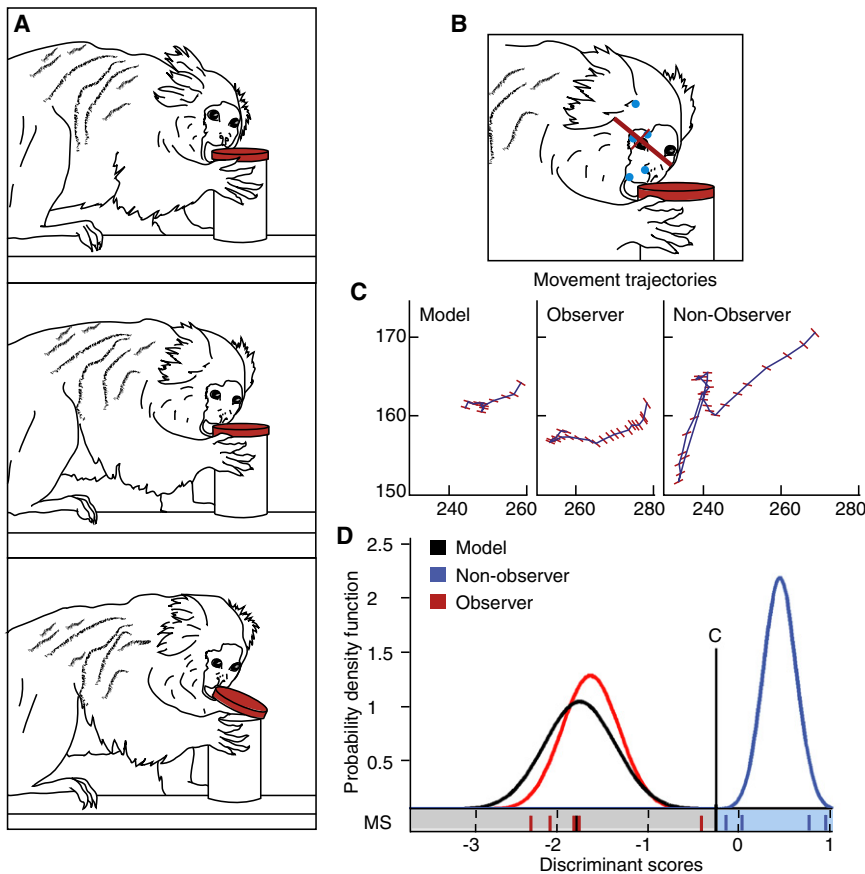


Figure 4. Marmoset Imitation

(A) Common marmosets precisely imitate a conspecific using a peculiar technique to open a food canister. Motion analysis confirmed the high copying fidelity of the observers.

(B) The head movement was calculated from the movements of five trace points (blue dots): (1) corner of the mouth, (2) outer corner of the nostril, (3) canthus, (4) corner of the white spot of the forehead, and (5) a corner at the base of the ear-tufts.

(C) One example each of the head position of the model, one observer, and one nonobserver in 1/25 s time intervals (red lines indicate head inclination) illustrate the high matching degree of model and observer, but considerable deviation of the nonobserver's, movement trajectory.

(D) The mean discriminant scores for movements of the observers were closer to the mean of the model than to the nonobservers in 99.96% of the cases (Voelkl and Huber, 2007).

in supporting cumulative culture. It is generally agreed that, to support cumulative culture, imitation must achieve a significant degree of copying fidelity and involve or enable learning, i.e., the acquisition of novel behavior (Heyes, 2009; Huber et al., 2009). Besides birdsong learning, it remains unclear whether other forms of animal social learning have the capacity to support cultural inheritance.

These issues have fueled the question of which species have the cognitive potential for imitation. Apes imitate in various forms (Whiten et al., 2004), but despite a century's efforts it remains unclear whether monkeys possess this ability (Fragaszy and Visalberghi, 2004). Although the sweet potato washing of Japanese macaques is a widely cited example of tradition formation in nonhuman animals, it is unclear whether social learning, let alone imitation, is involved. Furthermore, capuchin monkeys repeatedly fail to learn how to use an object as a tool by observation (reviewed in Fragaszy and Visalberghi, 2004). These findings led to a consensus view that culture is rare in primates, because true imitation is rare.

But recently, monkeys' inability to imitate has been challenged. Monkeys show cognitive imitation by copying an expert's use of a rule (Subiaul et al., 2004), recognize when they are being imitated (Paukner et al., 2005; Paukner et al., 2009), and imitate adult facial movements as neonates (Ferrari et al., 2006, 2009). Also, the discovery of mirror neurons (neurons that fire both when monkeys watch another animal perform a goal-directed

action and when they perform the same action) in rhesus monkeys suggests that they possess the neural framework for the matching system of imitation (Ferrari et al., 2009; Rizzolatti and Craighero, 2004). However, can monkeys also imitate *novel* behaviors (solving the transfer of skill problem)?

An observer's copy can vary greatly in its degree of matching to the model's template. So-called demonstrator-consistent responding implies that the subjects copied some part of the

observed actions. Interestingly, the largest body of evidence for action imitation again comes from birds (reviewed in Zentall, 2004). The most stringent test of whether animals can learn a new movement by observation involves the demonstration of at least one action that is unlikely to be performed, unless the subject had the opportunity to witness its performance (Bugnyar and Huber, 1997). Recent studies with common marmosets have provided evidence of very precise copying of new movements (Figure 4), challenging current theories of imitation in terms of associative learning, human-specific adaptations, and mirror neurons (Voelkl and Huber, 2000, 2007). Furthermore, recent evidence that archerfish seem capable of learning how to anticipate the path of moving aerial prey by observing a skilled conspecific suggests that precise movement copying might be widespread in the animal kingdom (Schuster et al., 2006).

Selectivity in Social Learning

An emerging theme in studies of the ability of animals to learn from others is that observers are selective in many respects, including what, when, and from whom to learn. This selective nature of social learning is buttressed by theoretical models of the adaptive advantages of social learning, which predict that organisms should copy when uncertain, copy the majority, and copy if better (Galef and Laland, 2005).

Species Show Differential Selectivity in What and Whom to Observe. Social learning is expected to occur in circumstances in which the observer can acquire new knowledge from others.

An individual must monitor the behavior of others with regard to affiliation, dominance, and tolerance to make the correct decisions of whom to solicit in agonistic conflicts, whom to groom, and whom to avoid. Monitoring the behavior of others is therefore a prerequisite for any form of behavioral adjustment during cooperation, competition, and communication. Whom you watch is also of crucial importance for the acquisition and spread of social information. However, time and/or habitat constraints limit an individual's opportunity to observe every other animal within the group or every action performed: observers must be selective. There are striking differences between species (Range et al., 2009; Range and Huber, 2007; Scheid et al., 2007), most of which are found in the attention-holding (duration of looks) rather than the attention-getting (frequency of looks) processes, which is more important for learning about the sequence and coordination of actions and their consequences.

Selectivity in Learning about the Environment. In addition to selectivity in the distribution of attention, selectivity may also depend on knowledge about the social and physical environment. To understand results of what others do, one needs to relate actions to effects. If the action itself is not copied, the environmental change must be understood in physical or causal terms and then reproduced by the observer's own means (emulation). By observation of a demonstrator successfully obtaining food, observers don't just learn to manipulate the tool, but also to use the tool for that function. This learning has been specified as learning about the operating mechanisms of objects or environment, properties of objects, relations between objects and functions, and the causal structure of the task (Byrne, 1998; Whiten et al., 2004).

For more than a decade, evidence for this kind of intelligent social learning was restricted to chimpanzees (Tomasello et al., 1987). Data from tool-using birds remain far from convincing in this respect (woodpecker finches, Tebbich et al., 2002; New Caledonian crows, Hunt and Gray, 2003). But keas, curious and manipulative mountain parrots, have proved able in the lab to selectively execute those actions from their motor repertoire that are sufficient for reproducing the observed effects (Figure 5, cf. Huber et al., 2001). This is especially interesting because keas have never been observed using tools in the wild. Perhaps animals that use tools may lack true causal understanding, but possess innate dispositions to manipulate certain objects, and an ability to learn during a sensitive phase early in ontogeny what effects these have (Tebich et al., 2002). Indeed, pigeons can learn about the consequences of a demonstrator's actions, without actually learning about the actions themselves (Zentall, 2004). Nevertheless, the translation of an observed environmental relationship into behavior that produces the same consequence is a quite remarkable cognitive ability, perhaps no less complex than imitation. It may be that a fascination with human-like imitation has deflected attention from equally valid and effective forms of social learning.

Intelligent Copying Requires Inhibition and Control. From a neurocognitive perspective, emulation may also entail the ability to inhibit or control copying others. In humans at least, such inhibitory processes depend on the functioning of the same higher-order brain centers that are involved in attributing mental states to others (Brass et al., 2009). In humans, these control

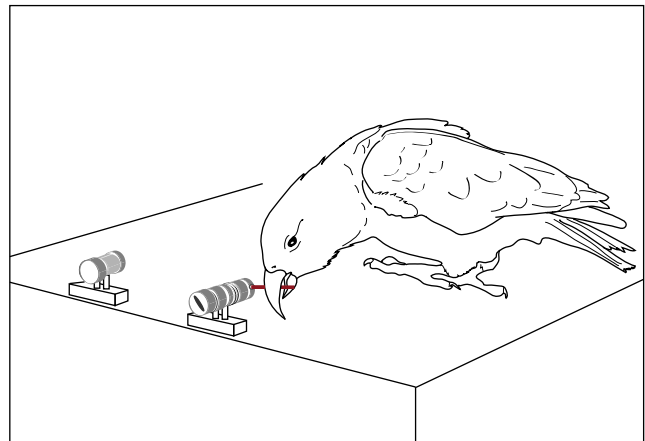


Figure 5. Kea Selectivity

Keas were allowed to observe a trained conspecific that demonstrated how to open a large steel box with rewards (toys). The lid of the box could be opened only after three locking devices had been dismantled (a bolt, a split pin, and a screw). The figure shows an observer pulling the metal split pin out of the screw in its first encounter with the box. Observers showed much greater success in opening the locking devices than nonobservers (Huber et al., 2001).

functions appear to be specialized for social interaction. But nonhuman animals have also demonstrated the ability to select intelligently just those pieces of information which are useful, neglecting details of behavioral form judged to be redundant or ineffective. When a human demonstrator showed several tool-using actions on a complex food container, using a mixture of effective and ineffective actions, young chimpanzees copied all actions only if they couldn't see the immediate effects of these actions. If they could, they ignored ineffective components, and predominantly tried effective ones instead (Horner and Whiten, 2005), suggesting that emulation is the favored strategy of chimpanzees when sufficient causal information is available.

Strategic Imitation Is Also Not a Human Specialty. For many decades, imitation studies focused on controlled, intentional (or "true") imitation because it was thought that imitation must be controlled in order to play an important role in cognitive and social development, or to mediate cultural inheritance. However, research on the chameleon effect in human adults (Chartrand and Bargh, 1999; van Baaren et al., 2009) and "overcopying" in children (Whiten et al., 2009) suggests that, even when control is limited, imitation can have systematic and far-reaching effects on cooperative behavior and the potential for cultural evolution.

One test for true imitation that controls for immediate, automatic (or "blind") copying is the deferred imitation test. Here, the animal is required to wait and engage in other behavior before replicating the previously seen actions. Recent evidence on this comes from dogs. Joy, a Weimaraner, performed at high levels of matching degree with delays shorter than 5 s, and once matched a familiar action even after 35 s (Huber et al., 2009). Strategic imitation also requires the observer to make sense of an action, and then recreate the most effective or rational solution. When confronted with demonstrated actions lacking a target object (vacuum actions, e.g., the human model jumping over nothing), Joy responded by performing an action which was functionally similar (jumping over a real hurdle standing nearby).

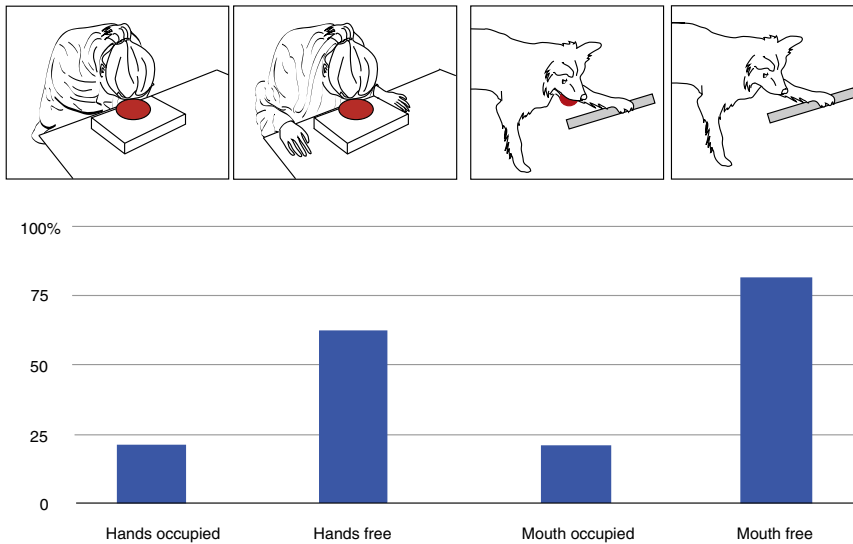


Figure 6. Rational Imitation in Children and Dogs

Both human infants and dogs evaluate the actions of others and decide whether or not to copy them. Children (or dogs) watched a model turn on a light box (or push a bar) by touching its top with her forehead, not her hands (or by pushing it down with a paw, not the mouth). If a model had a blanket wrapped around her body (or a ball in the mouth) during the demonstration (“occupied” condition), only about 20% of observers activated the box with their heads (or pushed the bar with the paw). The majority of the children (or dogs) used the hand (or mouth)—a more efficient way of turning on the lights (or depressing the bar). Perhaps they recognized that the model couldn’t use her hands (or the mouth) and had to use her head (or paw). But when the model performed the task without the blanket (or without the ball) (“free” condition), the majority of a second group of observers opted to copy the model’s head (or paw) movements, as if deciding that if the model did it, then it must be a better approach (Gergely et al., 2002; Range et al., 2007).

In studies using the so called “Do-as-I-do” paradigm (using chimpanzees, orangutans, parrots, dolphins, and dogs; reviewed in Huber et al., 2009), animals were not particularly sensitive to details of the actions, but instead attempted to achieve a functional fit. These species’ actions seem to be goal directed and object bound, and shortcuts reveal that they are often driven by efficiency. Interestingly, autistic children also show superior performance with object manipulations relative to body-oriented movements (Heimann et al., 1992).

Preverbal Human Children, Chimpanzees, and Dogs Exhibit Rational Imitation. The transmission of cultural knowledge requires learners to select what information to retain and imitate when observing others’ skills. Human imitative learning is a unique mechanism of naive pedagogy that facilitates fast and efficient cultural knowledge transfer, rather than a simple slavish reenactment of actions of a demonstrator. Fourteen-month-old human infants show evidence of this rational imitation ability (Gergely et al., 2002) and imitate peculiar actions only when the demonstrator had no obvious reason to execute them, suggesting that their imitation is a selective, interpretative (rational) process. They thus interpret others’ behavior as goal directed and, as a result, predict the most efficient action to achieve a goal. Early sensitivity to ostensive-communicative cues and to the efficiency of goal-directed actions is thought to be a crucial prerequisite for such relevance-guided selective imitation (Csibra and Gergely, 2009). Although this competence was previously thought to be human specific, recent experiments show an analogous capacity in dogs (Figure 6) and chimpanzees (Buttelmann et al., 2007; Range et al., 2007). As in human children, inferential competence seems not to require the attribution of mental states but relies simply on the evaluation of the observable facts: the action, the goal state, and the situational constraints.

Summary: A Rich Comparative Database for Studying Social Learning

Comparative research on social learning, vocal learning, motor imitation, and emulation provides a very rich set of models for understanding both the neural mechanisms and evolutionary

bases for both homologs and analogs of the mechanisms that support language and culture in our own species. The long-held belief that only humans and great apes can imitate has been challenged, suggesting that many taxa are living in an imitative universe. But outside of birdsong, the question of which species exhibit cultural patterns, particularly the cumulativity typical of human culture, currently remains a focus of vivid debate.

Testing Hypotheses about Language Evolution with Comparative Data

We end our review with some illustrations of the power of the cognitive phylogenetic approach to test hypotheses concerning neural mechanisms and evolutionary function.

The “Large Carcass” Niche: Parallels between Hominids and Ravens

In the course of hominid evolution, the proportion of meat in the diet increased, reflecting an increased importance of scavenging and hunting (Blumenschine and Selvaggio, 1988; Bunn and Kroll, 1986). Meat eating had important effects on nutrition and social behavior of hominid groups, long thought to be central in understanding the evolution of human cognitive and communicative skills (Dart, 1949; Lee and De Vore, 1968; Montagu, 1976). In particular, cooperative hunting, scavenging, and food sharing have been suggestive as powerful drivers of the information sharing capacity embodied in language (Isaac, 1978). Linguist Derek Bickerton has recently offered a quite specific hypothesis along these lines (Bickerton, 2010) and singled out one design feature of human language (Hockett, 1960) as both crucial and very rare: the capacity for displacement. Human language, unlike most animal signals, can convey information about objects or events that are not present. Bickerton proposes that the driving force behind this feature during hominid evolution was the need for cooperative scavenging of large carcasses, which would be too large to be moved, but so rich as to constitute a windfall for any primate group able to defend and butcher them. Bickerton proposes that the exigencies of this specific ecological niche drove the evolution of symbolic communication

in our lineage: “recruitment was ... the selective pressure that started protolanguage” (p. 209 of Bickerton, 2010).

Unfortunately, such hypotheses are difficult, if not impossible, to test solely on the basis of the archeological record, leading some commentators to dismiss them as untestable speculation (e.g., Lewontin, 1998). Taking the comparative perspective, however, displacement and recruitment are not unique to humans: precisely these functions lie at the heart of recruitment signaling in social insects, particularly the honeybee dance “language” (von Frisch, 1967). Paralleling social insects, we suggest that ravens, large-brained birds, support the idea that a scavenging lifestyle selects for socio-cognitive and communicative abilities.

Ravens Recruit Conspecifics to Scavenge Large Carcasses. Although ravens are omnivorous, they regularly feed on large mammal carcasses (Ratcliffe, 1997). Carcasses are rich but highly ephemeral food sources that are difficult to locate; moreover, they are often defended by predators or dominant conspecifics, and thus difficult to access by vagrant, nonbreeding ravens, who are generally subordinate to territorial breeding birds. Such subordinate birds cope with this challenge by teaming up (Heinrich, 1988; Marzluff and Heinrich, 1991). Ravens engage in two forms of recruitment: using nocturnal roosts as information centers (Marzluff et al., 1996; Wright et al., 2003) and attracting others via food calls (Bugnyar et al., 2001; Heinrich and Marzluff, 1991). The former strategy allows birds to search for food individually and cover a broad area (Dall and Wright, 2009). Upon encountering a food source, single birds remain silent, return to the nearest communal roost and return to the carcass the next day together with other birds (Heinrich, 1988). The number of ravens arriving at the new food source increases linearly over days, suggesting that one bird (most likely the finder) continues recruiting others until the source is depleted (Marzluff et al., 1996; Wright et al., 2003). Interestingly, the recruited individuals remain near one another at roosts (Wright et al., 2003), suggesting that certain birds group into temporary foraging bands.

Alternatively, ravens may use food calls at short distances. Younger birds (<5 years of age) give specific calls, “yells” (Heinrich, 1988) or “haa” calls (Bugnyar et al., 2001), when they encounter food that is difficult to access and/or feared. These calls develop from juvenile begging calls and are affected by hunger level (Heinrich and Marzluff, 1991) as well as the quality and quantity of a food source (Bugnyar et al., 2001): specifically, ravens call more often when hungry or when encountering preferred food, and stop calling once they manage to gain access to the food (Bugnyar et al., 2001; Heinrich and Marzluff, 1991). As in other species (e.g., Evans, 1997), food calling in ravens rests on a strong motivational basis. Nevertheless, because the timing and the location of calling signals the occurrence of food to listeners, it may be functionally referential (Bugnyar et al., 2001). Besides food calls, ravens give a variety of other calls during foraging that may provide information about feeding opportunities (Heinrich et al., 1993). These calls are not specific to the occurrence of food but are primarily given during food-related interactions (Bugnyar et al., 2001).

Although both food calls (Heinrich and Marzluff, 1991) and food-associated calls given during feeding (Heinrich et al., 1993) may attract nearby conspecifics, only food calls do so at

the appropriate time, i.e., when recruiting others is advantageous for overcoming territorial defense and/or neophobia. Food calling decreases with an increasing number of ravens gathering at the food source (Bugnyar et al., 2001), indicating an “audience effect” on the signaler. Adult territory holders may try to aggressively prevent nonbreeders from food calling (Heinrich and Marzluff, 1991), indicating some risk of punishment to callers. Possibly as a consequence, not all birds that encounter food behave similarly, and there is substantial individual variation in the number of calls given. Others must be within hearing distance for the food calling system to work. Otherwise, callers run the risk of attracting territory holders and facing punishment without increasing their chances of accessing food. Birds may thus be sensitive to the presence of other ravens and capable of adjusting their recruitment behavior accordingly.

Interestingly, in some areas, ravens typically search for food in loose groups and readily coordinate via calls upon encountering feeding opportunities (Bugnyar and Kotrschal, 2001; Dall and Wright, 2009). In other populations, individual search and long-distance recruitment at roosts seems to be the default strategy (Heinrich et al., 1994; Marzluff et al., 1996).

Testing the Recruitment Hypothesis with Ravens. The need to find ephemeral food, combined with the need to overpower food defenders, has led to a sophisticated system of information sharing in ravens. Birds both use cues given by successful foragers and actively signal the occurrence of food to others. The timing and location of food calling appears to provide functionally referential information to receivers. Moreover, ravens seem to be capable of flexibly controlling these signals, using long-distance recruitment and food calls only when appropriate. Such sophisticated call usage is probably learned.

The communication and cooperation of nonbreeding ravens to gain access to food sets the stage for another potential cognitive challenge: to share or secure food from others. Crowd-foraging ravens hardly share but carry off consecutive loads of food, which they scatter hoard at a moderate distance from the feeding site (Heinrich and Pepper, 1998). In such a situation, communication is counterproductive and one would expect strong selection for controlling behaviors and signals. Indeed, ravens are outstanding at deceptively withholding information (Bugnyar and Heinrich, 2006; Bugnyar and Kotrschal, 2002), potentially creating the selective force favoring judging others’ perspectives (Bugnyar et al., 2004) and knowledge states (Bugnyar and Heinrich, 2005).

Returning to Bickerton’s ideas about recruitment driving symbolic language, food calls do not constitute displacement, since the food is typically visible to the calling bird. However, the transfer of information that occurs at roosting sites certainly does qualify as displacement. Unfortunately, very little is known about how this communication occurs (but see Wright et al., 2003). Although ravens are difficult to observe at their roost sites, these birds are a living species that meets many of the criteria Bickerton lays out in his selective model for protolanguage in extinct hominids, and thus allow some of his predictions to be tested. For instance, we might expect birds informed of a carcass to react strongly, and negatively, if the carcass were not present the next day. If such behavior were repeated (as devious experimenters can easily arrange), a bird could experimentally be

branded as a liar. Similar manipulations of a carcass might allow us to probe the level of detailed information conveyed at roost sites, as has been done effectively in honeybees (Gould and Gould, 1988; Lindauer, 1971). In general, our understanding of raven communication remains quite rudimentary, but Bickerton's hypothesis offers both a reason for looking harder and some testable predictions about what information might be conveyed and why.

The Kuypers/Jürgens Hypothesis: Direct Connections Are Needed for Vocal Learning

Our second example hypothesis involves the neural circuitry underlying vocal learning. Neurons in the lateral motor cortex play a central role in human speech and song: destruction of the cortical face and larynx area abolishes voluntary learned vocalizations, but spares innate vocalizations like cry and laughter (Foerster, 1936; Groswasser et al., 1988). In contrast, lesions to motor cortex have no effect on vocalization in nonhuman primates (Aitken, 1981; Sutton et al., 1974), leading many researchers to posit two distinguishable neural control systems involved in vertebrate vocalization. The first is broadly shared and relies upon the midbrain periaqueductal gray as the center coordinating both the movements of the vocal production system and the emotional or motivational meaning of the calls produced. The second system is cortically driven, and is present in humans (and perhaps other species with voluntary control over complex, learned vocalizations), but not other primates (cf. Deacon, 1992; Jürgens, 1998; Jürgens et al., 1982; Myers, 1976).

What specific differences between these two circuits might underlie their different uses for controlling learned and innate vocalizations? A first clue came from a series of pioneering studies by the comparative neurologist Hans Kuypers. Kuypers compared cortical projections to brainstem motor nuclei in humans and other mammals by combining experimental lesions with Nauta/Gygax staining of degenerating axons to map the descending connections from cortex to the brainstem and spinal cord (Kuypers, 1958a, 1958b; Kuypers, 1973). Based on 4 human stroke victims, 4 chimpanzees, and 17 macaques, he found that primates have direct monosynaptic connections from cortex to a variety of motor nuclei, while cats possess only indirect, multisynaptic connections. Direct cortical connections may underlie the greater precision and voluntary control primates have over their faces, tongues, and limbs. However, Kuypers observed degenerating axons in the nucleus ambiguus, which encompasses laryngeal motor neurons, only in human brains. This observation was extended by Jürgens et al. (1982), who observed prolonged mutism in a stroke victim after bilateral cortical lesions. When an equivalent lesion was experimentally induced in a squirrel monkey, no changes in its vocalizations were observed, though it lost control of its jaw, lips, and tongue. The primate observations have been confirmed with modern tract tracing (cf. Jürgens, 2002), and the human results have been replicated in an additional stroke patient (Iwatsubo et al., 1990). These converging data provide strong support for the Kuypers/Jürgens hypothesis: that direct connections from motor cortex onto the primary motor neurons controlling the vocal apparatus, especially the larynx, are necessary to support complex learned vocalizations. Given these neuroanatomical differ-

ences between humans and nonhuman primates, which correlate perfectly with the behavioral lack of vocal learning in other primates, this hypothesis is quite plausible. But is it testable?

Testing Kuypers/Jürgens in Vocal Learning Species. Because vocal learning has evolved independently in multiple vertebrate lineages, the answer is yes. Vocal learning of complex songs appears to have evolved convergently in three bird lineages (songbirds, parrots, and hummingbirds, Jarvis, 2004; at least four mammalian clades: humans, seals, cetaceans, and bats, Janik and Slater, 1997; Knörnschild et al., 2010; and, as suggested by recent data, elephants, Poole et al., 2005). If the Kuypers/Jürgens hypothesis is correct, members of these species should have direct connections between telencephalic neurons and the primary vocal motor neurons in the brainstem, and such connections should not be present in related clades incapable of vocal learning.

Songbird data are consistent with these predictions. Birds lack a neocortex and produce sound using a novel organ, the syrinx, and we must adapt the hypothesis to adjust for these fundamental differences. Tract tracing studies show that cells in the final songbird motor region in the pallium (homologous to mammalian cortex) indeed send direct monosynaptic projections to the motor neurons controlling the syrinx whose cell bodies lie within the lower brainstem (Wild, 1993, 1997). Such direct connections are not present in subsocial birds, the closest songbird relatives that do *not* learn their songs. These avian data thus are consistent with the Kuypers/Jürgens hypothesis.

A skeptic might correctly observe that the differences between birds and mammals, both in terms of neuroanatomy and vocal production, make this a less than fully convincing case. Fortunately, there are now at least three nonhuman mammalian clades that are known to vocally imitate. All of these have neocortex, and at least two of them (bats and seals) use the "standard" mammalian vocal apparatus (lungs and larynx) to create their vocalizations. Although there are nontrivial issues involved in tract tracer studies in these species, the predictions of the Kuypers/Jürgens hypothesis are clearly amenable to further testing.

Mirror Neurons and Language Evolution

Our third example involves mirror neurons, one of the more fascinating neuroscientific findings in the last few decades (di Pellegrino et al., 1992; Rizzolatti and Craighero, 2004). Mirror neurons were initially discovered in macaques in the context of hand movements and visual perception, and the discovery of mirror neurons was seen by some as support for the gestural protolanguage hypothesis: the idea that hominids evolved language in the gestural domain before the evolution of spoken language (Arbib, 2005; Hewes, 1973). Because apes have good imitative abilities for manual gestures, in contrast to their inability to mimic sounds, mirror neurons might have provided a preexisting neural substrate for signal learning in the LCA of humans and apes. However, the discovery of macaque mirror neurons that respond to the sound of actions cast some doubt upon this conclusion (Kohler et al., 2002), as does the fact that the macaque monkeys studied have poor imitative abilities in either gestural or vocal domains (cf. Fitch, 2010).

The argument that mirror neurons imply a gestural protolanguage has been further weakened by the discovery of audiovisual mirror neurons in songbirds (Prather et al., 2008). In two

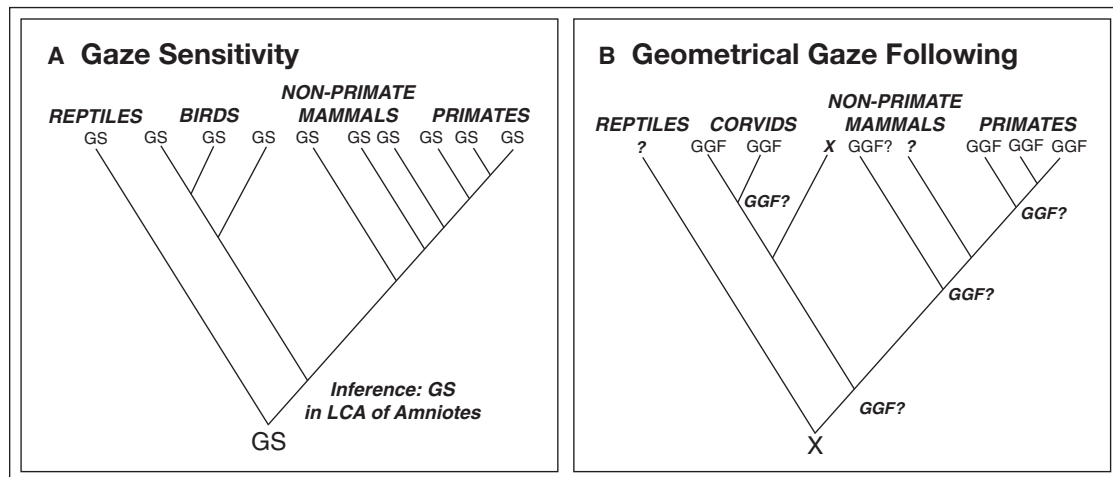


Figure 7. A Preliminary Cognitive Phylogeny for Gaze Processing

(A) The widespread occurrence of gaze sensitivity (GS) implies the presence of GS in the LCA of all amniotes.

(B) In contrast, the scattered distribution of gaze following (GF) and geometric GF (GGF), based on current knowledge, leaves open the possibility of convergence in birds and mammals, or homologous descent from an early amniote.

species of songbird (swamp sparrows and Bengalese finches), neurons in the higher vocal center (HVC) fire both when the bird sings certain syllable types and when it hears these types sung. These auditory mirror neurons are thought to represent a corollary motor discharge used to sharpen the match between motor and auditory output. Mirror properties were found only the subpopulation of HVC neurons that project to Area X, a striatal nucleus important in song learning, suggesting that they play a role in song acquisition and maintenance. These observations suggest that any form of sensory motor integration can be supported by mirror neurons, which can flexibly develop in the brain of vertebrates capable of vocal imitation. It is thus unclear what implications mirror neurons have, if any, for the phylogenetic timing of the human capacity for vocal learning. Again, convergently evolved birdsong provided the crucial test case.

The FoxP2 Gene Has Been Repeatedly Recruited in Vocal Learning Circuits

Finally, research into the genetic basis of human speech and birdsong learning has provided an intriguing new indication of the relevance of research on birdsong to the evolution of human language. Recent research has strongly implicated the importance of the transcription factor gene *FoxP2* in human speech, because clinical data show that speech production is severely disrupted when this gene suffers a missense mutation (cf. Vargha-Khadem et al., 2005). In songbirds, *FoxP2* is upregulated in nuclei involved in song learning (Haesler et al., 2004), and reduction of *FoxP2* expression levels in song nuclei of zebra finches leads to less accurate, incomplete song learning (Haesler et al., 2007), providing direct evidence for the importance of *FoxP2* in vocal learning across species.

Given that humans and birds evolved vocal learning convergently and have significant differences in both neural architecture and vocal production, it was quite surprising to find that the same gene plays a causal role in these species. This appears to be another example of “deep homology” in which the development of convergent structure is mediated by homologous

genes (Gehring and Ikeo, 1999; Shubin et al., 1997). *FoxP2* seems to be the first example of deep homology in a gene involved in spoken language (cf. Fitch, 2009b). Why should re-use of a transcription factor occur? Scharff and Haesler (2005) suggest that *FoxP2* plays a functional role in procedural motor learning in all vertebrates, and that this circuitry is “exapted” when species evolve vocal learning, a hypothesis consistent with the fact that similar song nuclei appear to have evolved (or been co-opted) in the separate evolution of vocal learning in hummingbirds, parrots, and songbirds (Jarvis, 2004).

The *FoxP2* gene has only started to yield its secrets, and we can expect much more to be learned from a broad comparative approach. In mice, successful genetic manipulations of *FoxP2* provide a powerful tool to begin exploring, in detail, the role of this gene in the developing mammalian brain (Enard et al., 2009; Groszer et al., 2008; Shu et al., 2005). Intriguingly, bats appear to have undergone powerful selection on the *FoxP2* gene, leading to an unparalleled *FoxP2* diversity in this order (Li et al., 2007). Although little is known, at present, about the function of *FoxP2* in the bat brain, the recent discovery of complex vocal learning in a bat (Knörnschild et al., 2010) suggests that bats may also have much to teach us about the function of this gene in mammalian vocal control.

Summary

We have reviewed the evidence in animals for multiple mechanisms underlying human social cognition. The picture is not simple: we find various abilities dotted about the vertebrate phylogenetic tree in a complex pattern that defies easy description. In some cases (e.g., simple gaze detection), we find abilities in a broad variety of species, and are tempted to declare this basic form of social intelligence a shared vertebrate homolog. In others (e.g., geometric gaze following), the very restricted evidence currently available suggests scattered examples of convergent evolution. However, in many cases, we lack adequate data to conclusively decide whether a result found in

(say) corvids and apes is a convergent analog, or a widespread homolog: the crucial data from other vertebrates are unavailable. Thus, for many traits, broader comparative data sets will be required to support clear conclusions.

Figure 7 illustrates our approach, providing a preliminary cognitive phylogeny of vertebrate gaze processing. Basic gaze sensitivity has been observed in virtually every species tested, suggesting that this is a basic vertebrate capability. Provisionally assuming that gaze sensitivity is homologous in these species, we infer that it was already present in the LCA of amniotes about 340 million years ago. Gaze following has also been observed in many species, but examples are currently limited to birds and mammals. This leaves two options: that avian and mammalian gaze following evolved convergently, or if they are homologs, that gaze following was also present in the common ancestor of living amniotes. The crucial data for resolving this involves further research on social cognition in reptiles (tortoises, lizards, crocodylians); without such data, either option seems equally likely. Finally, regarding geometrical gaze following, strong data exists now only for corvids, apes, and dogs; again convergence or homology are possible. What we can conclude for certain, contra an older tradition expecting only primates to be “sophisticated gaze followers” (Tomasello and Call, 1997), is that geometric gaze following either evolved convergently in corvids and dogs OR is much more ancient, either in the LCA of mammals or possibly even the LCA of living amniotes.

Although the cognitive phylogenetic approach highlights the need for more data, one thing that is clear is that a linear scala naturae approach to cognition, where animal intelligence is expected to increase with phylogenetic proximity to humans, can be firmly rejected. We have focused on data from birds and other nonprimate animals to emphasize this fundamental point. A modern approach to comparative cognition must fully embrace a tree-oriented approach, firmly rooted in Darwin’s conception of life as one vast family tree, if it is to make sense of cognitive evolution. The now-abundant data indicating highly developed cognition in birds poses a clear challenge to the primate-centered viewpoint that has dominated psychology and neuroscience for the last century; birds are currently neck-and-neck with the smartest primate in many tests of both social and physical intelligence (cf. Emery and Clayton, 2004). Indeed, we have argued here that the best parallels for some aspects of language and culture are to be found not in other primates, but in songbirds. How such high levels of cognitive performance are generated in brains a fraction of the size of those of most mammals remains a fundamental puzzle for computational neuroscientists, suggesting perhaps that mammalian neocortex is not the most efficient computational substrate available among vertebrates. But our purpose here is not to place birds on a pedestal; rather, we aim to show how a very wide variety of species, from tortoises to dogs, can both inspire new hypotheses about cognitive evolution and provide multiple ways to test such hypotheses.

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