19.1 Evolving a Theory of Mind

Humans have the ability to attribute mental states to others; that is, to attempt to predict others’ knowledge, desires, beliefs and their consequences. To summarize these capacities, Premack and Woodruff (1978) introduced the term “Theory of Mind” (ToM). They called it a “theory” as mental states are not directly observable and therefore need to be inferred. ToM-related skills can be differentiated into three classes: understanding others’ perception (e.g., attention, visual or auditory perspective, etc.), understanding others’ motivation (e.g., others’ goals, intentions, etc.) and understanding others’ knowledge (e.g., others’ beliefs).

In recent years the question whether nonhuman animals, like humans, have social cognitive capacities became the focus of comparative cognitive research. From an evolutionary perspective, it is most likely that humans share some social cognitive skills, perhaps including mental state attribution, with other species. The so-called “social intelligence hypothesis” formulated by Humphrey (1976) hypothesizes that cognitive capacities are most likely an adaptation to life in complex social groups. In fact, the more complex a social group’s structure, the more its constituent individuals can benefit from understanding the other group members’ cognitive states. This is because it will allow the individual to make flexible decisions depending on its understanding of the social relationships, and hence to adapt quickly to the constantly-changing social environment. Later, the Machiavellian Intelligence hypothesis, formulated by Whiten and Byrne (1988), added competition as an important driving force for the evolution of social cognitive skills in social species. This hypothesis states that life in groups, and especially competition over resources, puts a constant selection pressure on evolving flexible cognitive skills. As there is a constant struggle to outwit competitors to monopolize resources, Whiten and Byrne hypothesized that social cognitive skills evolved in a kind of arms race between the evolution of measures to manipulate others and the evolution of countermeasures to avoid such manipulation.

If living in complex social groups is seen as the driving force for the evolution of social cognition, then we should expect to find social cognitive capacities, similar to
humans', in group-living animals. In recent decades, an important question was therefore to what degree humans share our social cognitive capacities with other animals.

Humans can, in some situations, make predictions and inferences about others' mental states. Humans can predict what others have or have not seen, what others desire, what they believe, and so forth—all often summarized as a "Theory of Mind" (ToM). While some researchers believe that reasoning about mental states is a uniquely human skill, others argue that humans share some social cognitive skills, including mental state attribution, with other species—notably our closest living relatives, the chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). From an evolutionary perspective, certain social cognitive skills would be beneficial for group-living animals, as they are for humans. Following the Machiavellian Intelligence hypothesis, individuals with some knowledge about others, and the capacity to attribute mental states to others, would be in a better position to outwit their competitors; hence, group living should put a premium on the evolution of social cognitive skills that allow a more flexible understanding of others. However, there are many group-living species, of which few, if any, are thought to have a capacity to attribute mental states to others. This raises the question whether other processes (e.g., associative learning) are sufficient to navigate social groups, even absent a full-fledged ToM.

In order to study the evolutionary history of a certain skill, it is essential to compare the cognitive capacities of different species. For example, to investigate abilities that are particular to humans and our evolutionary history, we need to isolate those that are unique to humans amongst our closest phylogenetic relatives, the other apes. Any cognitive ability that is part of a shared repertoire between related species is likely to be part of their shared evolutionary inheritance from their last common ancestor. When it comes to the evolution of ToM-related skills, the interesting question is whether a complex understanding of others is a widespread phenomenon in the animal kingdom, or whether it is a cognitive capacity unique to humans or shared only with a few other (perhaps closely related) species. While this question remains unresolved, evidence has recently accumulated suggesting that at least one ability—knowing when others can or cannot see things—may be a cognitive domain in which the capacities of some animal species are similarly flexible to those of humans.

### 19.2 Reading Others’ Attention

Eye-shaped stimuli are important signals in the animal kingdom. One good example for the importance of eye-shaped signals in the animal kingdom is the Peacock butterfly (*Inachis io*), which has eye-shaped spots on its wings to scare away potential predators. These eyespots are an effective morphological antipredator adaptation that significantly increases individuals' chances of survival (Vallin, Jakobsson, Lind, & Wiklund, 2005), suggesting that attention to eye-like patterns is widespread and can be exploited. However, individuals from this species are most likely not aware that they have this signal. They have very limited control over its presentation to potential predators. They cannot modify the signal based on whether or not the potential predator is in a position to see them. The interaction between both individuals (prey and predator) can
therefore be best explained as one example of a sender–receiver relationship in which one individual, the sender, presents a certain signal to which the other individual, the receiver, responds. The sender’s signals, as well as the receiver’s response, are fixed patterns, shaped by selection processes during evolution. The Peacock butterfly likely has no understanding whatsoever of the predator’s mental states.

However, there is evidence that for some species, the eyes signal something about others’ attentional states. All great ape species—including chimpanzees, bonobos, gorillas, and orangutans—adjust their gestural communication to the attentional state of a human experimenter. When the human is attentive (e.g., has her head turned towards the subject) they use more visible gestures (such as pointing or reaching) than when the human is not attentive (e.g., has her head turned away). Chimpanzees also use different types of gestures depending on the attentive state of the receiver. They use audible (e.g., hand clapping) instead of visible gestures if others are nearby, but not in a position to see them (Kaminski, Call, & Tomasello, 2004; Liebal, Call, & Tomasello, 2004; Liebal, Pika, Call, & Tomasello, 2004) and use visible gestures (e.g., pointing) when the other is in the position to see them and their eyes are visible (Hostetter, Russell, Freeman, & Hopkins, 2007).

Sensitivity to the eyes as an important signal for others’ attention seems to be widespread in the primate family. Rhesus monkeys (Macaca mulatta) and also ringtailed lemurs (Lemur catta), for example, steal less food from a human experimenter whose eyes are open or directed toward them than from one whose eyes are closed or oriented away (Flombaum & Santos, 2005; Sandel, MacLean, & Hare, 2011).

Differentiating others’ attentional states is also not restricted to primates and seems to be present in species more distantly related to humans as well. Dolphins (Tursiops truncatus) produce more “pointing” (here defined as alignment of the body while remaining stationary for over 2 seconds) if a human is in a position to see them (e.g., oriented toward them) than when he/she is not (Kikyo, Gori, & Kuczaj, 2004). Dogs (Canis familiaris) also show a high sensitivity to human eyes. When tested in a competitive situation with a human, in which the human forbade them to take a piece of food, dogs took more food when the human was oriented away from the food than when he was oriented toward it, or when the human’s eyes were closed as opposed to when they were open, or when the human was distracted as opposed to attentive (Call, Bräuer, Kaminski, & Tomasello, 2003). This was not only true in competitive, but also in more cooperative, contexts in which the dogs had to decide which human to beg from. Here, the dogs directed their begging more toward a human whose eyes were visible than toward a human whose eyes were covered (Gácsi, Miklósi, Varga, Topál, & Csányi, 2004). There is also evidence that different bird species are sensitive to a human’s attentional state. Sparrows and jacksdaws attend to the presence of the eyes as well as the gaze direction of a human in a competitive situation related to food: When the human’s eyes were closed or averted, starlings resumed feeding earlier, at a higher rate, and consuming more, whereas jacksdaws were responsive to subtle cues of attention, depending on the social context (i.e., whether the individual was a stranger or familiar to them) (von Bayern & Emery, 2009).

Overall, this shows that a certain level of sensitivity to the status of the eyes is relatively widespread in the animal kingdom among species very distantly related to each other. This could be an indicator that sensitivity to being observed might be an evolutionary ancient and relatively hard-wired behavior with an urgent evolutionary
function, but might also suggest that this trait is not homologous in all species and evolved as an analogous trait separately and several times in the animal kingdom.

### 19.3 Following Others’ Gaze

Many species from different taxa not only differentiate whether or not they are being observed, but also attend to where others are looking. For socially living animals, following the gaze of others is beneficial in order to gain information about outside entities. By following another’s gaze, the individual can get valuable information about different resources including food, predators, etc. One way to test for this behavior is to see whether an individual follows the gaze direction of another to a specific target outside its own field of view. Various primate species follow the gaze direction of other individuals. For example, all great apes species readily follow the gaze direction of a human experimenter (Bräuer, Call, & Tomasello, 2005). In this study, the human experimenter suddenly shifted her gaze toward the ceiling. Gaze-following behavior in this situation was compared to a control condition during which the experimenter looked straight at the opposite side of the room. Apes looked at the ceiling significantly more often when the human had looked up than when she had not, indicating that they were sensitive to human gaze direction. The ability to follow others’ gaze is present not only in apes, but also in various monkey species more distantly related to humans. Emery, Lorincz, Perrett, Oram, and Baker (1997) showed that rhesus macaques were able to locate an object according to the gaze direction of a conspecific depicted on a TV monitor. Tomasello, Call, and Hare (1998) tested several monkey species (including Soopy mangabeys, Cercopithecus atys torquatus, Rhesus macaques, Macaca mulatta; Stumptail macaques, Macaca arctoides; and Pigtail macaques, Macaca nemestrina) for their ability to follow the gaze of their group members. An experimenter located in an observation tower, attracted the attention of one individual by presenting food to her. Once this individual had shifted her gaze toward the food, it was recorded whether a nearby subject (that had not seen the food itself) would respond with co-orientation to the conspecific’s gaze shift. All monkey species tested in this setting followed the gaze direction of their conspecific. There is also evidence that different New World monkey species, like cotton-top tamarins (Saguinus Oedipus), common marmosets (Callithrix jacchus) and different lemur species, are responsive to the gaze direction of others (Burkhart & Heschl, 2006; Sandel et al., 2011).

Gaze following is thus widespread among the primates. However, like attention reading, it has also been shown in a wide variety of other mammals including dolphins, seals (Arctocephalus pusillus), goats (Capra hircus), and dogs and wolves (Canis lupus). Dolphins and seals spontaneously attend to the gaze direction of humans (indicated by head direction) in a food search game (Scheumann & Call, 2004; Tschudin, Call, Dunbar, Harris, & van der Elst, 2001). Goats, like primates, follow the gaze of their conspecifics, and dogs seem to be especially sensitive to a human’s eyes and gaze direction (Kaminski, Ricciol, Call, & Tomasello, 2005). Apart from the mammalian species tested, there also seems to be evidence that species even more distantly related to humans are sensitive to others’ gaze direction. Ravens (Corvus corax) and rooks (Corvus frugilegus) have been shown to follow others’ gaze direction. Ravens have been shown to co-orient with the gaze of a human experimenter from an
early age. In this test, a human experimenter shifted gaze (head and eye direction) up to a distant location to which the ravens responded with co-orientation (Schlögl, Kotrschal, & Bugnyar, 2007). Recently it was also found that red-footed tortoise (Geochelone carbonaria), a solitary living species, follow the gaze of their conspecifics (Wilkinson, Mandell, Bugnyar, & Huber, 2010). This is especially interesting, as another line of research suggests that gaze-following skills may be more sophisticated in species with more complex social structures compared to less socially complex species from the same family. Gibbons, for example, seem to have less sophisticated gaze-following skills than those of great apes, possibly a result of their lack of social complexity as a monogamous species (Liebal & Kaminski, 2012). Conversely, ringtailed lemurs show more gaze-following skills compared to other members of the strepsirrhines, possibly as an adaptation for living in the most complex of strepsirrhine social groups (Sandel et al., 2011).

Taken together, these data show that gaze and gaze direction are important stimuli for a number of species widespread in the animal kingdom. This again suggests a very urgent evolutionary function for gaze following, with a high adaptive value for diverse species. Most likely, the ability to follow gaze helps individuals exploit others for information about important resources like food, mating opportunities, etc. However, the fact that gaze following, like attention reading, has emerged in very distantly related species may suggest that this trait is not homologous in all species, and separately evolved as an analogous trait several times in the animal kingdom.

One important question is to what extent the classical gaze-following behavior—that is, shifting one’s gaze direction in response to seeing another individual’s gaze shift—a is a more or less learned or inherent automatic response, or truly an indicator of one individual’s attention to another individual’s “line of sight.” If the latter, does this suggest attention to what that individual is seeing, and hence to the other individual’s psychological state? One way to test this is to consider the following prediction: If an individual interprets gaze as an indicator of another individual’s line of sight, it should, if necessary, relocate to a position from which it can see what the other is looking at. There is evidence that at least some species seem to follow others’ gaze not just as an automatic response, but by truly attending to what others are looking at. This is shown by the fact that those species take some effort to track the other’s gaze direction to a specific target (by moving towards it) instead of automatically looking in the same direction. Tomasello, Hare, and Agnetta (1999) showed that chimpanzees walk around a barrier in order to track a human’s gaze who had just looked behind this barrier. Brüuer et al. (2005) showed that all great apes follow the gaze of a human experimenter behind a barrier by walking around the barrier, presumably to track the human’s line of sight. There is also evidence that non-primate species are able to track a human’s line of sight. Wolves seem to follow other individuals’ gaze around barriers (Range & Viranyi, 2011) and ravens, like apes, will move around a barrier presumably to see what a human is looking at (Bugnyar, Stöve, & Heinrich, 2004).

However, following gaze around barriers still does not necessarily indicate a deeper understanding of seeing in others. Subjects do not have to interpret the other individual’s mental states to be successful in this task. Instead of mentally representing that the other individual is seeing something differently, animals may simply have the motivation to look at the same spot the other individual is fixating. Following gaze around barriers may thus indicate representations of spatial relationships, but not necessarily of other minds.
19.4 Perspective Taking

Some mammalian species seem to understand when others' visual access to an object or event is blocked. To test whether chimpanzees have what Flavel, Shipstead, & Croft (1978) define as “Level 1” perspective taking, researchers set up a situation in which two chimpanzees, one dominant over the other, have to compete over two pieces of food. The subordinate chimpanzee, which would normally not have had a chance to gain food with the dominant present, had an advantage: While it had visual access to both pieces of food, the dominant individual could see only one, the other being hidden by a wooden barrier. When given the chance to make a choice, the subordinate chimpanzee preferred to approach the piece of food behind the barrier—the one the dominant could not see—to the piece in the open, visible to the other individual. When the chimpanzees were alone, they chose randomly between the two pieces indicating that their preference for the hidden piece was not merely based on a preference for eating behind an obstacle. In another control condition, the authors showed that chimpanzees would not prefer a piece of food behind a transparent barrier, which potentially protected them from the competitor physically, showing that their preference for the barriers is not due to it being an obstacle that potentially protects them physically (Hare, Call, Agnella, & Tomasello, 2000).

There is also evidence from other mammalian species that they may have some understanding of when others' line of sight is blocked. Goats and also domestic dogs seem to distinguish between two pieces of reward based on whether another individual has visual access to it or not (Kaminski, Bräuer, Call, & Tomasello, 2009; Kaminski, Call, & Tomasello, 2006). Domestic dogs, for example, distinguish which toy to bring based on the human's visual access to those toys. In this paradigm, the human and the dog sat opposite each other with two toys between them. One toy was placed behind an opaque barrier such that the experimenter had no visual access to it. The other toy was placed behind a transparent barrier such that both the experimenter and the dog had visual access to the toy. Upon the command to fetch, dogs preferred to fetch the toy that was visible to the experimenter. They fetched the visible toy significantly more in this condition than in a control condition where the dog and the experimenter sat on the same side of the barriers and thus had comparable visual access to both toys (Kaminski, et al., 2009). Whether this is based on a true understanding of others' psychological states or based on more simple mechanisms will be the subject of future studies. However, that at least the chimpanzees' behavior cannot be explained by simply perceiving others' eyes as an aversive stimulus is shown by another study. In this study, the chimpanzees are in competition with a human whose eyes they cannot see. The chimpanzees then have to make the decision whether to reach for food through an opaque or a transparent tunnel. As the chimpanzees cannot see the humans' eyes while reaching, their decision has to be based on whether or not the human can potentially see their hand in the tunnel. As chimpanzees prefer to reach through the opaque tunnel, these results suggest that chimpanzees based their behavior on some sensitivity to the visual perspective of the other individual (Melis, Call, & Tomasello, 2006) and did not follow a simple rule, "avoid the piece of food associated with the eyes of the competitor."

From an evolutionary perspective, it is interesting that birds (specifically, corvids), a group of species very distantly related to primates, seem to possess a flexible understanding of others' visual perspective very similar to that of primates. Evidence
suggests that these birds seem to have a flexible understanding of others' psychological states, allowing them to form flexible strategies to reduce the probability of others stealing from their hidden caches of food. Scrub jays (*Aphelocoma californica*) and ravens differentiate situations during which they have been observed hiding food from situations where they were able to cache privately (Bugnyar, 2011). When scrub jays have a choice of where to cache while a conspecific is observing, they prefer to hide food in locations which are relatively far from the observer. They also prefer to cache behind an opaque barrier, or in a tray located in the shade, to caching in the open or in a tray located in the light (Dally, Emery, & Clayton, 2004, 2005). The sophisticated cognitive abilities of members of the corvid family, which are very comparable to those of primates, are seen as a good example for analogous evolution as a result of similar selection pressures in the environment. One hypothesis is that it is the complexity of their social environment which put a premium on the evolution of social cognitive skills in corvids, as it has done in primates (Emery, 2004).

19.5 Knowledge Attribution

There is, therefore, plenty of evidence that different animal species understand something about others' current visual perspectives. There is evidence for attention reading, gaze following, and even perspective taking. However, there is also evidence some few species, mainly apes and corvids, not only understand something about others' current visual access, but also about that in their past. One well-known paradigm is the so-called "guesser–knower" paradigm first introduced by Povinelli, Rulf and Bierschwale (1994). The authors conducted a series of experiments which tested whether chimpanzees could take into account what a human had seen in the immediate past. To test this, they confronted chimpanzees with a situation in which they had to distinguish between two human experimenters who informed them about the location of hidden food. One of the experimenters (the knower) witnessed food being placed in one of several containers while the other experimenter (the guesser) waited outside the room. After the guesser reentered the room, the two humans (guesser and knower) pointed to different containers. The chimpanzee was then allowed to choose between the containers, and could potentially base her choice on the information coming from the most reliable source, the knower. In this setting, chimpanzees could only differentiate between humans after several hundred trials, which was most likely the result of discriminating between whether the human was present or absent during baiting. However, one general critique of this paradigm is that it is rather unnatural for chimpanzees: A human indicates the location of food in a very cooperative manner, something that would not occur in a group of chimpanzees. It is highly unlikely that one chimpanzee would indicate the location of food to another chimpanzee with the intention of letting her have it. Kaminski, Call and Tomasello (2008) therefore created a paradigm based on chimpanzees' natural tendency to compete over food. In this paradigm, two individuals, subject and competitor, sat opposite one another, with a sliding board between them that a human could slide back and forth. Each trial began with a hiding event, in which food was hidden under one of three cups while both chimpanzees were watching. Another piece of food was hidden under a second cup, while only the Subject was watching. Hence, while the locations of both pieces of food were
known to the Subject, only one of them was known to the Competitor. In some trials, the Competitor was given the first choice with the Subject unable to see this choice being made. After the Competitor had made its choice, it was the Subject’s turn. The chimpanzees in this situation preferred the piece of food unknown to the Competitor, presumably because they understood that the other piece, the one the Competitor had information about, was likely to be gone by the time of their own choice. Chimpanzees were similarly successful in this paradigm to six-year-old children and adult humans (Kaminski et al., 2008). This finding therefore supports previous studies showing that chimpanzees may take into account what others have seen in their immediate past (Hare, Call, & Tomasello, 2001).

Scrub jays, like chimpanzees, seem to understand others’ knowledge states. Dally Emery, and Clayton (2006) presented subjects with a situation in which they had to decide which tray to recover hidden food from. Earlier, the birds were allowed to hide food in one tray in the presence of observer A, with a second tray present but covered. After a delay, the subject was allowed to cache in the other tray with observer B present. After another delay, the subject was given the opportunity to recover their caches from both trays, and had to make the decision which cache to recover based on which observer was present. Interestingly, the birds specifically recovered the caches that observers had seen them make and did not recover any cache if observed by a completely naïve individual, suggesting that it was not simple presence/absence guiding their behavior (Dally et al., 2006). Similar evidence comes from ravens, who seem to be able to predict others’ behavior based on what they had observed them observing (Bugnyar, 2011).

19.6 Understanding Others’ Beliefs

One ability that is seen as a benchmark for mental state attribution, and therefore theory of mind, is the understanding that others have beliefs and that those beliefs can be true or false. Having an understanding that another individual’s belief is false requires an understanding that another person’s mental states can be contradictory to one’s own and, more importantly, contradictory to reality. So far, there is no evidence that any nonhuman animals can make this distinction.

In one version of a false belief task, chimpanzees were again confronted with a situation in which two individuals had to compete over food. Two chimpanzees sat opposite each other with a sliding board between them, on top of which were three identical cups. The subject, however, had exclusive access to an additional cup to choose from, which was placed sideways to the subject. Two different types of reward were hidden: a preferred high-quality reward was placed in one of the cups on the table between the subjects, and a less-preferred low-quality reward was placed in the additional cup next to the subject. After the initial baiting, which both subjects observed, the high quality reward was manipulated a second time. During this manipulation, the experimenter either lifted the reward and placed it back in its original location or shifted it to a new location. This second manipulation was either witnessed by the competitor or not. Hence, in one of the conditions (the “shift unwitnessed” condition) the competitor has a false belief about the location of the high-quality reward. The competitor was always the first to choose, and the subject did not see the competitor
choosing but had to base her decision on what she guessed the competitor had done. It turned out that in this setting, subjects did not make the distinction between situations in which the others’ belief was true or false (Kaminski, et al., 2008). This is one study of several, all of which indicated that, despite the fact that chimpanzees (and other animals) understand knowledge and ignorance in others, they may not fully appreciate that others have mental representations of the world (Call & Tomasello, 1999, 2008; Kaminski, et al., 2008; Krachun, Carpenter, Call, & Tomasello, 2009).

19.7 Conclusions

Certain social cognitive skills, like reading others’ attentional states and following others’ gaze directions, seem to be relatively widespread throughout the animal kingdom. This shows that gaze direction and the status of others’ attention are a meaningful cue for many socially living animals. However, some of those skills (e.g., gaze following) appear to be automatic reflexive responses which do not necessarily involve any flexible understanding of others’ psychological states. The fact that some of these traits are widespread in the animal kingdom suggests that they possess a high survival value, for example, by aiding in the rapid location of predators or avoiding conflict. Other skills, such as the ability to take another’s perspective or understand what others have seen in the immediate past, do not seem to be so widespread, and thus may be based on more complex cognitive operations.

However, whether any of these studies can show that animals truly attribute mental states to other individuals is still a highly controversial issue. One criticism of all the studies mentioned above is that the animals in those studies may simply base their strategies on associations formed during the experiment or in earlier life, or have simply read others’ behavior and acted based on that information. Instead of having some concept of seeing, animals may simply learn to associate the eyes of their competitor with one piece of food and not the other. The stimulus “eye” may be seen as an aversive stimulus, which the subject then associates with the food, and therefore avoids (the so-called “evil eye hypothesis”). Even though most recent studies try to rule out this associative account, it remains a question whether subjects in those studies need to refer mental states to others in order to solve the problem.

Another nonmentalistic interpretation of the results is that animals do not form concepts of others’ mental states but rather about others’ behavior, and that this is sufficient to succeed in all paradigms used with animals so far (Tovinelli & Vonk, 2004). This line of thinking suggests that animals follow certain behavioral rules, which they have learned over time: For example, “every time I do x, my conspecific reacts by doing y.” The weakness of this approach is that it is not the most plausible explanation across all of the very different studies and paradigms which exist and which provide evidence for animals’ understanding of others’ psychological states (see Call & Tomasello, 2008 for a discussion of this point). However, all evidence to date also shows that there are strong limits to animals’ understanding of others. While some species represent others’ knowledge states, such as what they may have seen in their immediate past, no nonhuman animal has yet demonstrated the ability to attribute false beliefs to others. This suggests that a truly representational theory of mind may be a uniquely human cognitive capacity.
From an evolutionary perspective it is interesting that the most convincing evidence for flexible social cognitive skills comes from two very distantly related groups of species: apes and corvids (Clayton, Dally, & Emery, 2007; Emery & Clayton, 2009). This is interesting, as the morphology of mammalian and bird brains is so substantially different that apes and corvids skills are almost certainly convergent rather than homologous processes (Emery & Clayton, 2009). Similar social cognitive skills therefore may be an adaptation to similar socio-ecological challenges in the social life of these species, for example, in navigating competition over resources and life in a complex social society.

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