## Do You Know What I See? Visual Perspective Taking in Nonhuman Animals

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ABSTRACT. Visual perspective taking is not only an essential skill for effective visual communication (Emery, 2000), but also an indicator of the presence of social cognition and theory of mind in nonhuman animals (Heyes, 1998). In this paper, we review some of the prominent experimental paradigms and research findings on visual perspective taking in various nonhuman species, such as the begging task, the guesser-knower task, and competitive paradigms. However, in spite of the plethora of research that has been done, it still remains inconclusive as to whether or not nonhuman animals are capable of visual perspective taking due to the varied and contradictory findings of past studies. Several possible explanations exist for these discrepancies, which include varying definitions of the term "perspective taking," the lack of attention given to species-specific ecological validity, confounding variables such as associative learning and visual-spatial skills, differences in the experimental set-up and release time in competitive paradigms, and the lack of close replications. It is suggested that future research should aim to overcome the challenges of this area of study so as to be able to develop an empirically sound understanding of visual perspective taking in nonhuman animals.

The social intelligence hypothesis (Kummer, Daston, Gigerenzer, & Silk, 1997) or the Machiavellian intelligence hypothesis (Byrne & Whiten, 1988) proposes that due to the social competition for resources and mates, evolution has favoured individuals who were able to successfully predict and manipulate the behaviour of others. One mental operation that is suggested to have evolved out of this social competition is the ability to understand the perspectives and psychological states of others (MacLean & Hare, 2012). Interestingly, the social intelligence hypothesis is not unique to humans, as it is proposed that social intelligence can be expected to have evolved in any species that display the following criteria: large brain relative to body size, the presence of large and long-lasting social groups, and a long life span (Tomonaga, Uwano, Ogura, & Saito, 2010). A number of animal species meet these criteria, such as certain primates, corvids, bats, elephants, hyenas, and cetaceans (Tomonaga et al., 2010). This then poses the question: are nonhuman animals capable of understanding the mental states of others?

Theory of mind refers to "the capacity to make lawful inferences about the behaviour of other agents on the basis of abstract, theory-like representations of the causal relation between unobservable mental states and observable states of affairs" (Penn & Povinelli, 2007, p. 732). However, because theory of mind is a phenomenon that cannot be directly perceived, but rather, must be inferred from behaviour (Povinelli, Dunphy-Lelii, Reaux, & Mazza, 2002), a major challenge to its study is identifying behaviours that provide sufficient evidence for the existence of such higher order cognitions. Heyes (1998) proposes that among the most promising approaches to the study of theory of mind and social cognition among animals are perspective-taking tasks.

Visual perspective taking is defined as "the ability to appreciate what others can and cannot see" (Held, Mendl, Devereux, & Byrne, 2001, p. 1338). Researchers in the field of comparative psychology have long been interested in understanding visual perspective taking among nonhuman animals, as being able to perceive the attentive state of another is an essential skill for effective visual communication (Emery, 2000). This is because successful transmission of a

signal is not only dependent on the sender's ability to produce the signal, but also on the recipient's ability to perceive the signal (Emery, 2000). This is particularly critical for visual communication, whereby the receiver must not only be in close proximity, but must also be oriented toward, and attentive to, the sender (Gacsi, Miklosi, Varga, Topal, & Csanyi, 2004). As such, determining whether nonhuman animals are capable of visual perspective taking, and understanding the various cues that they use to infer the perspective and attentive state of another would shed light on how these species are able to successfully communicate in the wild. However, beyond its functional importance, visual perspective taking also bears inferential significance, as the ability to take on the visual perspective of others is said to be one of the most promising indicators of the presence of social cognition and theory of mind in nonhuman animals (see Heyes, 1998). Thus, given that visual perspective taking could potentially unveil the answer to the pivotal question of the existence of theory of mind in nonhuman species, it is no wonder then that researchers have consistently been striving to develop experimental methodologies that are capable of adequately testing for visual perspective taking in nonhuman animals.

While much is already known about the development of visual perspective taking in humans, concrete evidence of such ability in nonhuman species still remains elusive despite extensive research (Heyes, 1998). In a review of experimental methodology for primate social cognition, Hare (2001) highlights that arguably the biggest challenge of studying perspective taking among nonhuman species is that animals are nonverbal. In human developmental psychology, the study of perspective taking has relied almost exclusively on participants' ability to verbally communicate what he or she knows, such as in the classic "false-belief" task that is commonly used among children (Hare, 2001). In contrast, researchers of nonverbal animals must rely on behavioural measures through which perspective taking abilities can be convincingly inferred (Hare, 2001). As such, there is often no way to be certain that the behaviours demonstrated are the result of the ability to understand what others can and cannot see, and thus, the findings of such studies are often subject to many alternative explanations. In light of this, researchers have sought to develop various experimental paradigms, all with the common goal of attempting to better understand visual perspective taking among nonhuman animals.

One of the oldest approaches to studying visual perspective taking among animals is the guesser-knower task that was first introduced by Premack in 1988. In this task, the subject watches as an experimenter places a piece of food into one of two containers that are located behind an opaque screen such that the subject is unable to see directly which of the containers is being baited. The subject also has visual access to two trainers – one trainer ('knower') can see which container is being baited, but the other ('guesser') cannot because the screen is blocking its view. Once the container is baited, the subject is then allowed to ask one of the two trainers for 'advice' on which container has the food, and the trainer responds by pointing to one of the two containers, after which the subject choses between the two containers. The critical test in this task is whether or not the subject would be able to discriminate which of the two trainers had witnessed the baiting and therefore knew where the food was. In Premack's (1988) original study, four chimpanzees were tested; two consistently chose the informed trainer ('knower'), while the other two did not have a clear preference for either trainer. Despite the small sample size and the inconclusive findings, Premack's (1988) study was nonetheless a momentous one, as the basic approach to the guesser-knower task has continued to be used in the study of visual perspective taking of many other species (see Cooper et al., 2003; Povinelli & Eddy, 1996; Povinelli, Nelson, & Boysen, 1990).

However, in spite of its widespread use, the guesser-knower task is not without its criticisms. Among the major limitations to this approach is that success on the task can be attributed to more parsimonious explanations of associative learning, and thus, may not be an adequate test of higher order cognition (Held et al., 2001). In addition, the use of human trainers also poses further threat to the validity of this task. Firstly, by using humans instead of conspecifics, experimenters are expecting subjects to be able to interpret the behaviours of another species (Held et al., 2001) – this is not only irrelevant to successful visual perspective taking among conspecifics, but may also be a tall order. Second, because both trainers know their roles as either the 'guesser' or the

'knower,' it is hard to ascertain that they are not unconsciously providing cues to the subject as to which of them is the 'correct' choice.

Seeking to refine the guesser-knower task and examine visual perspective taking among a lesser-studied species, Held et al. (2001) conducted a study using domestic pigs. In this study, ten pigs were trained to move from a starting point into one of four corridors that they had previously seen a human enter while carrying a bucket containing food. During these training sessions, subjects received food rewards for choosing the right corridor. In subsequent transfer tests, the subject being tested could not see the corridors, but could see two conspecifics in individual start boxes on its left and right - one had visual access to the corridors and the baiting, while the other did not. The two companion pigs were released and the subject was observed to see which of the two companions it followed. Subjects were not rewarded for their performance on the transfer tests, to minimize the possibility of associative learning (Held et al., 2001). Furthermore, because the conspecifics did not know which was the correct answer for the test subject, it is unlikely that either the 'guesser' or the 'knower' could have provided cues to the subject (Held et al., 2001). The results revealed that out of nine subjects (one subject was removed from statistical analysis), eight of the subjects followed the 'knower' at a frequency that was below chance level - a finding that Held et al. (2001) attributed to specific corridor preferences. Only one pig showed a significant preference for the 'knower,' in line with behaviour that is expected of one who is able to take on the visual perspective of another (Held et al., 2001).

However, Maginnity and Grace (2014) highlight that in tasks that require subjects to rely on human cues, species such as chimpanzees and pigs may be at an inherent disadvantage, simply by virtue of their lack of social interactions with humans. In contrast, domestic dogs would be the perfect species for such a procedure, as they have extensive socialization with humans and are sensitive to many human cues (Maginnity & Grace, 2014). Thus, in a series of well-controlled experiments based on the guesser-knower task, Maginnity and Grace (2014) tested domestic dogs on whether they would be able to discriminate between a human trainer who saw the container being baited and one who could not because the trainer was absent during the baiting (Experiment 1), covered her eyes during the baiting (Experiment 2) or gazed away from the container during the baiting (Experiment 3). In all conditions, the dogs showed a significant preference for the container that was pointed to by the 'knower,' thus suggesting that dogs are sensitive to cues that are indicative of human attentional states (Maginnity & Grace, 2014). Therefore, Maginnity and Grace (2014) emphasize that the failure of other species on the guesser-knower task in past research may not be due to their inferior cognitive abilities, but rather, the lack of ecological validity of the methods employed to test for them.

Comparable findings have also been obtained in studies that have used a similar approach – the begging task. Yet another classic approach to studying visual perspective taking, the begging task, was originally developed by Povinelli and Eddy (1996) in their study of chimpanzees. In this task, subjects are required to beg for food from one of two human trainers - one whose vision is obscured (e.g., by wearing a blindfold or having a bucket over the head) and one who is able to see (Povinelli & Eddy, 1996). The rationale behind this task is that if subjects were able to understand the visual perspective of others, they would beg preferentially from the trainer who could see their begging actions and therefore respond by providing food, as opposed to the trainer whose vision is obscured (Povinelly & Eddy, 1996). While studies involving chimpanzees have failed to convincingly demonstrate their ability to engage in visual perspective taking (Povinelli & Eddy, 1996), studies on dogs appear to yield much more promising results in that dogs preferred to beg for food from the human who could see (Cooper et al., 2003; Gacsi et al., 2004; Udell, Dorey, & Wynne, 2011). However, interestingly, their behaviour changed depending on the way in which the person's vision was obscured – for example, they were more likely to ignore a person who was reading a book than a person who had a bucket over his or her head (Cooper et al., 2003). Given the fact that the dogs' behaviour varied simply as a function of the object that was used, Udell et al. (2011) highlight a critical question - do dogs succeed on this perspective-taking task because they possess theory of mind, or is their success simply a demonstration of associative learning from prior experience with humans?

Several researchers have argued that dogs do

not acquire these skills due to prior experience, but rather, as a species as a whole, dogs have evolved "human-like social skills" during the course of domestication (Hare & Tomasello, 2005). If such an argument is true, then domesticated dogs should outperform undomesticated canids on this perspective-taking task, regardless of the age or prior experiences of the dog being tested (Udell et al., 2011). However, if such a genetic predisposition is not necessary, then both domesticated dogs and undomesticated canids should be able to learn to beg preferentially from humans who can see based on prior experiences of receiving rewards from attentive humans (Udell et al., 2011). Therefore, Udell et al. (2011) devised a study to examine whether hand-raised wolves (who had been reared by humans since infancy and had regular contact with humans), pet dogs (who also had regular interactions with humans) and shelter dogs (who had minimal interactions with humans) would perform differently on the perspective-taking begging task.

The results of their study revealed that similar to domesticated dogs, wolves were also capable of succeeding on the begging task, demonstrating the ability to behave in accordance with a human's attentional state (Udell et al., 2011). In addition, it was also shown that in the initial stages, the shelter dogs were not as sensitive to the attentional states of humans as compared to pet dogs, though this behaviour improved with subsequent trials (Udell et al., 2011). Udell et al. (2011) then suggest that these findings demonstrate that dogs' success on perspective-taking tasks cannot be attributed to domestication alone, and neither can they be taken to imply the possession of higher order social cognition; rather, they assert that "Dogs' ability to follow human actions stems from a willingness to accept humans as social companions, acquired early in ontogeny, combined with conditioning to follow the limbs and actions of humans to acquire reinforcement" (Udell et al., 2010, p. 328). The findings of Udell et al. (2011) demonstrate a significant point in the research of social cognition among animals; that is, it is overly simplistic to merely ask whether or not a species displays behaviours that support the presence of social cognition, but rather, it is important to take into consideration the specific conditions under which these behaviours are demonstrated. By doing so, research would be able to shed light on the possible origins of these behaviours, and

thus provide clearer insight as to whether such behaviours are truly evidence of higher order social cognition, or simply the product of associative learning.

If tasks that rely on interactions with humans have high ecological validity for dogs, what then would be a suitable research paradigm for other species? Hare (2001) suggests that for chimpanzees, the answer may lie in their competitive nature. In contrast to dogs whose selective pressures have encouraged cooperation with humans, chimpanzees' lives revolve heavily around intense competition with conspecifics for resources (Hare, 2001). Therefore, it can be expected that chimpanzees' social cognitive abilities were evolved out of the need to out-compete their conspecifics; thus, such abilities would most likely be displayed in a competitive situation (Hare, 2001).

Among the studies that have made use of chimpanzees' natural tendency to compete is an experiment by Hare, Call, Agnetta, and Tomasello (2000). In a nutshell, the experiment involved a dominant and a subordinate chimpanzee that were competing for food. The subordinate could always see where the food was being hidden, while the dominant chimpanzee could see the food being hidden in one condition, and in another condition, could not (Hare et al., 2000). The results revealed that when the dominant chimpanzee could not see the food being hidden, the subordinate went for the food; however, when the dominant chimpanzee had seen the food being hidden, the subordinate refrained and stayed back (Hare et al., 2000). The findings indicate that the subordinate chimpanzee had an understanding of what the dominant chimpanzee could and could not see - thus, the subordinate knew that, when the dominant chimpanzee could not see the food being hidden, it did not know where the food was, and it would be safe for the subordinate to go for the food (Hare et al., 2000). However, if the dominant chimpanzee had seen the food being hidden and therefore knew where the food was, the subordinate would have to compete with the dominant for the food, and as a result, chose to stay away (Hare et al., 2000).

Further research by Brauer, Call, and Tomasello (2007) aimed to examine the specific factors that would influence chimpanzees' behaviour in competitive situations, and it was found that it was not merely the presence of competition, but the intensity of the competition that was a crucial factor. Brauer et al. (2007) conducted an experiment that was similar to that of Hare et al.'s (2000), but surprisingly, the subordinate chimpanzees in their study showed no preference for the food that was hidden from the dominant's view. Instead, the subordinate was able to successfully obtain the food regardless of whether or not it could be seen by the dominant chimpanzee (Brauer et al., 2007). This contradicting result led Brauer et al. (2007) to hypothesize that the spatial arrangement of the experimental set up had reduced the competitiveness of the situation in comparison to that of Hare et al. (2000). This was due to the fact that in the present study, the food was placed in closer proximity to the subordinate chimpanzee (Brauer et al., 2007). Thus, knowing that it had an advantage over the dominant chimpanzee, the subordinate tried to obtain as much food as possible (Brauer et al., 2007). To test this hypothesis, Brauer et al. (2007) conducted a second experiment in which the food was now placed in closer proximity to the dominant chimpanzee. As hypothesized, the subordinate showed a clear preference for the food that was out of sight of the dominant, thus providing further support for the conjecture that chimpanzees are capable of demonstrating visual perspective taking in competitive situations (Brauer et al., 2007).

However, in line with the notion that the intensity of the competition is an important factor in influencing the subordinate's behaviour, it is crucial to note that the procedures of Hare et al. (2000) and Brauer et al. (2007) differed in terms of the amount of time between the release of the dominant and subordinate chimpanzees. In Hare et al.'s (2000) study, both the dominant and subordinate chimpanzees were released into the room at the same time, while Brauer et al. (2007) only released the dominant chimpanzee once the subordinate had entered the room. This difference in release time would likely have made the situation in Brauer et al.'s (2007) experiment less competitive than that of Hare et al. (2000), thus making it difficult to compare and interpret the results across studies.

Beyond chimpanzees, competitive paradigms have also been found to be useful in the study of other competitive species, such as goats (Kaminski, Call, & Tomasello, 2006) and long-tailed macaques (Overduin-de Vries, Spruijt, & Sterck, 2014). Using an experimental paradigm similar to that of Hare et al. (2000),

Kaminski et al. (2006) examined the visual perspective taking abilities of domestic goats. However, given that goats in the wild live in complex social groups and have been known not only to compete with one another but also to form alliances and hierarchies, Kaminski et al. (2006) additionally took into account the relationship between the specific two subjects being tested. The results revealed that the subordinate's behaviour relied heavily on whether or not it received demonstrations of aggression from the dominant goat (Kaminski et al., 2006). Subordinates who were treated aggressively showed a significant preference for the hidden food, while those who did not receive aggression preferred the visible food (Kaminski et al., 2006). As a result, subordinates who did not receive aggression ended up obtaining more food - they first obtained the visible piece of food, followed by the hidden piece of food (Kaminski et al., 2006). Although this behaviour may seem to contradict the findings of Hare et al. (2000) and Brauer et al. (2007), Kaminski et al. (2006) suggest that these findings do in fact provide support for goats' ability to engage in visual perspective taking - the reason being that the subordinate knew what the dominant could and could not see, and thus, knew that the visible food was at greater risk of being taken by the dominant in comparison to the hidden piece (Kaminski et al., 2006). Therefore, in order to secure the maximum amount of food, the subordinate went for the visible piece first (Kaminski et al., 2006). However, when the dominant goat posed a threat to the subordinate by behaving aggressively, the subordinate preferred the hidden piece so as not to have to compete with the dominant.

It is important to note that in contrast to Hare et al. (2000) and Brauer et al. (2007), the dominant goat in Kaminski et al.'s (2006) study was only released once the subordinate had chosen between the two pieces of food. Thus, because the subordinate was likely to have been able to reach the visible piece of food before the dominant, subordinates who did not receive aggression significantly preferred to go for the visible piece of food first. Similar results were obtained by Overduin-de Vries et al. (2014) in their study of long-tailed macaques, as it was found that subjects who were faster significantly preferred to go for the visible piece of food first, followed by the hidden piece of food, thereby securing both pieces; however, those who were slower showed a preference for the hidden food. Taken together, these findings suggest that in more naturalistic competitive situations, animals such as chimpanzees, goats and long-tailed macaques are capable of understanding what others can and cannot see, and use this information to their advantage.

Much research has been done to examine visual perspective taking among primates and dogs, but what about humans' more evolutionarily distant relatives? In contrast to chimpanzees, dolphins are phylogenetically distant from humans, with the closest common ancestor of humans and cetaceans living over 65 million years ago (Browne, 2004). However, dolphins have large brains relative to their body size, with certain species such as the bottlenose dolphin having much larger brains than chimpanzees, and coming in second only to humans in terms of brain size (Browne, 2004), thus making them possible candidates of social intelligence (Tomonaga et al., 2010).

Few studies on perspective taking have been done among cetaceans, one of which is a study by Tomonaga et al. (2010), which aimed to examine whether bottlenose dolphins were sensitive to their trainers' attentional states. This study involved four male bottlenose dolphins that lived in captivity and were well trained to follow their trainers' hand gestures. They were then tested to determine whether they would respond to their trainer's hand signals if their trainer was in a position that implied inattentiveness, such as facing their back toward the dolphin or having a bucket placed over his or her head. The results of the study revealed that overall, the dolphins did not respond any differently to the different attentional states demonstrated by their trainer, and continued to obey the hand signals for positive reinforcement. However, because these dolphins were raised in captivity and were well trained to obey these hand signals, the interpretation of these findings remains uncertain (Tomonaga et al., 2010). Although it is possible that the dolphins' lack of attention to their trainers' attentional states implies the inability to engage in visual perspective taking, it is highly likely that their continued obedience to the trainers' hand signals were the result of having been extensively trained to obey the human trainer. Thus, further research is necessary to examine whether these behaviours still hold true in situations that allow for more spontaneous reactions (Tomonaga et al., 2010).

More recently, interest has also been directed toward other non-primate species, one of which is the African elephant. African elephants live in a complex network, and as such, communication is essential in their everyday interactions (Smet & Byrne, 2014). Although elephants do not use visual signals as their primary means of communication, research has shown that elephants do respond to subtle visual signals (Smet & Byrne, 2013) and are capable of producing communicative gestures as well (Poole & Granli, 2009). To better understand African elephants' ability to infer the attentional states of others, Smet & Byrne (2014) conducted a study with 10 captive African elephants. In this experiment, the elephants were first exposed to an experimenter who would call the elephant's name, place a piece of fruit on a tray, and then move the tray toward the elephant's reach for it to obtain the fruit (Smet & Byrne, 2014). After three days of these 'no-delay' trials, the elephants were then tested with 'delay' trials whereby, after placing the fruit onto the tray, the experimenter pretended to forget to move the tray toward the elephant - leaving it out of reach of the subject (Smet & Byrne, 2014). During this delay, the experimenter adopted one of several facial and body orientations that implied either attention or inattention (Smet & Byrne, 2014). It was observed that the elephants made significantly more experimenter-directed gestures when the experimenter's face and body were directed toward them as compared to when the experimenter was facing away (Smet & Byrne, 2014). In addition, these gestures were produced significantly more frequently when the experimenter was present versus absent, thus demonstrating that these behaviours were not random, but were dependent on the presence of an experimenter who could perceive them (Smet & Byrne, 2014).

In spite of the plethora of research that has been done on visual perspective taking, it still remains inconclusive as to whether or not animals are capable of visual perspective taking, due to the varied and contradictory findings of past studies. Several possible explanations exist for these discrepancies, one of which is that the interpretation of research findings varies in accordance with the definition of the term "perspective taking" and the context in which it is used. For example, Held et al. (2001) refers to perspective taking as "the ability to appreciate what another can and cannot see" (p. 1338), while Hare (2001) defines perspective taking as the ability "to consider and react to another's perceptions, desires and beliefs as opposed to just their behaviour" (p. 272). Note that while Held et al. (2001) refers solely to visual perspective taking, Hare's (2001) definition refers to a much broader context that involves the understanding of another's cognitions. In light of this difference, the conclusion of whether animals are capable of engaging in perspective taking would undoubtedly be dependent on the definition of the term "perspective taking" that one is referring to.

Besides that, although there has been an increased focus on ensuring internal validity of experimental methodology, limited attention has been paid to species-specific ecological validity (Hare, 2001). Considering the incredible diversity of animals, it would be overly simplistic to assume that all nonhuman species would respond in a similar manner. As such, low ecological validity makes it difficult not only to test for visual perspective taking, but also to generalize the findings to a real world setting (Hare, 2001). This could possibly explain why certain species may appear to demonstrate visual perspective taking abilities when tested on one task, but not on another. Therefore, it is important for researchers to understand the unique niche of different species and to take advantage of these differences in their study of visual perspective taking. As evidenced by dogs' success on tasks that involve interaction with humans (Cooper et al., 2003; Gacsi et al., 2004; Maginnity & Grace, 2014; Udell, et al., 2011) and chimpanzees' success on competitive tasks (Brauer et al., 2007; Hare et al., 2000), ensuring the ecological validity of experimental paradigms would likely help to unravel the seemingly varied and contradictory findings of past research.

In addition, a nonverbal paradigm also makes it difficult to account for other confounding variables that could potentially influence subjects' behaviour on the task. This prevents researchers from being able to convincingly rule out alternative explanations and conclude with certainty that a subject's success on an experimental task is indeed due to the ability to engage in visual perspective taking. Arguably one of the biggest confounding variables is the possibility of associative learning, which is a major challenge to designing an effective experiment on visual perspective taking. Because subjects are often obtained from zoos, research centers or from volunteer pet owners, the life histories of the subjects are rarely known to the researchers, thereby making it difficult to account or control for prior learning or experiences in their own home environments (Elgier, Jakovcevic, Mustaca, & Bentosel, 2012). This is of significant consideration, as novel behaviour is a key factor in providing support for the use of higher order cognition that goes beyond simple associative learning (Elgier et al., 2012).

To illustrate, dogs have been found to be successful on the begging task, whereby they beg preferentially from the attentive human rather than the inattentive human. However, such behaviour could possibly be due to associative learning from experiences with their owner - for example, at a dinner table, pet dogs are more likely to receive food from a person who can see the dog begging, which then causes them to form an association between begging from an attentive person and receiving food (Udell & Wynne, 2008). In contrast, the life experiences of shelter dogs are strikingly different, as they are often ignored by workers and visitors (Horowitz, 2011). As a result, shelter dogs may come to learn that the attentional state of a human is of no significance to them (Horowitz, 2011), subsequently leading to poor performance on the begging task. Unfortunately, past experiences of the subjects may very well be an inherent and unavoidable confound, as Held et al. (2001) highlight that "any possible design that would discount these possibilities [of prior learning] would also stack the odds heavily against the development of mental state attribution even if subjects had the potential. Test animals would have to be kept in social isolation, to be able to categorically rule out pre-experimental learning of the relationship between seeing and subsequent behaviours in others, without understanding what the seer knows" (p. 1351).

Besides prior learning, animals' performance on perspective taking tasks could also be confounded by other cognitive abilities, such as visual-spatial skills. In their study of chimpanzees' understanding of their own visual experiences, Krachun and Call (2009) found that chimpanzees were able to successfully maneuver themselves around occluded objects in order to see them. In contrast to studies involving another individual, there were no gaze or behavioural cues that the chimpanzees could have relied on (Krachun & Call, 2009). This success demonstrates that chimpanzees have an understanding of the spatial relations between themselves and objects in their environment, suggesting that they are capable of knowing what can be seen from different angles and positions (Krachun & Call, 2009). Although it still remains unclear as to whether chimpanzees employ a comparable strategy when deducing the visual perspective of others, this then raises the question of whether visual-spatial skills are confounding, or even necessary, factors for successful visual perspective taking. Could animals' poor performance on visual perspective taking tasks be attributed to inferior mental rotation, as opposed to the inability to understand the mental states of others? Such questions provide further avenues for future research.

Finally, the diverse findings of various studies could also be the result of differences in the methodology employed by different researchers. As demonstrated by Brauer et al. (2007), even slight changes in the set up of the experimental room led them to obtain strikingly different results from Hare et al. (2000), the very researchers from whom they adopted the competitive paradigm. Further research revealed that the change in the spatial arrangement of the room had altered the competitiveness of the situation, which in turn, affected the behaviour of the subjects (Brauer et al., 2007). If even minor differences in methodology could result in contradicting findings between studies that employed the same experimental paradigm, it should come as no surprise then that studies using different research paradigms have yielded such a wide array of results. This highlights the importance of taking such differences into consideration when comparing findings across studies, as well as the significance of conducting close replications in the guest to better understand visual perspective taking among nonhuman animals.

In conclusion, the social intelligence hypothesis (Kummer et al., 1997) posits that visual perspective taking can be expected to have evolved in all animal species that possess a large brain, long-lasting social groups, and a long life span – suggesting that animals such as chimpanzees, dolphins, dogs, and elephants have the capacity to understand and appreciate the perspectives of others (Tomonaga et al., 2010). However, despite the abundance of research that has been carried out to examine the visual perspective taking abilities of nonhuman animals, the inconsistent methodologies as well as the varied and contradictory findings of past research render them inconclusive. Thus, future research should aim to overcome the challenges of this area of study so as to be able to develop an empirically sound understanding of visual perspective taking in nonhuman animals.

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