Spring 2015

Sociality of Gaze Following in Black and White Ruffed Lemurs: Following a Live Person versus a Photograph

Hannah Sterling Mason
Bard College

Follow this and additional works at: https://digitalcommons.bard.edu/senproj_s2015

Part of the Cognitive Psychology Commons

Bard

Sociality of Gaze Following in Black and White Ruffed Lemurs: Following a Live Person versus a Photograph

Senior Project Submitted to

The Division of Science, Mathematics, and Computing

of Bard College

by

Hannah Mason

Annandale-on-Hudson, NY

May 2015

Acknowledgements

First and foremost I would like to thank the staff at the Trevor Zoo for letting me work so closely with the lemurs. You gave me a great opportunity, which I would have enjoyed even if it wasn't for a grade, and you were so much more kind and helpful to me throughout the year than I could ever have hoped for.

Of course I have to thank my prized lemurs Fidget and Bombo, even though your little brains will never let you read this. Even if I couldn't get any significant results from you, your cooperation and enthusiasm made this whole project possible.

I would also like to thank my senior project board – Sarah Dunphy-Lelii, Frank Scalzo, and Tom Hutcheon. You had all the right questions and comments that really helped to shape my project and my write-up of it. Please give me a good grade!

I especially want to thank my senior project advisor Sarah Dunphy-Lelii. It was really gracious of you to start working with me in a tutorial last year so I wasn't completely starting my research from scratch. I always dread getting comments back from you on my writing but only because you push me to do my best! You have kept me on track this whole year, even when I didn't think it was possible, and that means a lot to me.

Thank you to the Lifetime Learning Institute, to David Shein, to Bard's Psychology Department, and to the Transportation Office for giving me the means to get to the zoo and back every week for testing. I really would not have been able to complete this project if it were not for all of your support.

Thank you to my reliability coder Grace Shu – I had so much trouble with my video recordings but you did a really great job with them.

I also want to thank Philip Johns – may the memory of him teaching at Bard rest in peace. You introduced me to the whole concept of studying animal behavior, and to the Trevor Zoo, and of course to the data analysis program JMP, which is infinitely better than SPSS and nobody from the Psychology Department will ever convince me otherwise. I really wish you could have been on my board (love you actual board members).

Of course my wonderful housemates at the Milkshack deserve some credit, as do our honorary housemates and family members. This year has been exciting to say the least, and you all helped me through it and gave me the positivity I needed to keep working.

And last but not least, thank you to my friend and eternal study buddy Jonian Rafti for letting me work with him in the student government office for the whole second semester. Please work in the real government!

Abstract

One measure that is commonly used to assess a species' mental complexity is its gesture-following ability, or the ability to follow a human gesture (such as a gaze or a point) to choose between potential food sources. Animals that have demonstrated this ability include dogs and primates. The high-level explanation of gesture following is that it signifies an animal's ability to understand the human's knowledge of where the food is and his intent to communicate that knowledge. However, gesture following could also be explained as being a low-level mechanism relying on directional bias. Looking at the eyes of another individual is an extremely adaptive instinct; even if no perspective taking is involved one is still more likely to find objects of universal interest such as food or threats. For my senior project, I investigated the phenomenon of gaze following in black and white ruffed lemurs at the Trevor Zoo in Millbrook, NY. Specifically, I tested the legitimacy of the gaze following paradigm as a measure of social cognition by comparing lemurs' gaze following of a live person versus a photograph of a person versus a photograph of another lemur. The live person is a more reliable social partner reacting to the environment as it changes. The photo, on the other hand, is a static, abstract representation of a social partner and an indirect communicative gesture made by the true social partner, but that happens to correspond visually with the live gaze cue. The photograph of the other lemur is meant to control for possible differences in response to faces of same and other species, as well as to replicate previous findings that lemurs were able to find hidden food based on gaze information from a photograph of a conspecific. I hypothesized that the lemurs would be able to follow gaze to find hidden food, and that this gaze following would be due to perspective taking. Therefore I expected the lemurs to find the food more often than chance in all conditions, and to find food most often in the live gaze condition. My subjects were not able to find the hidden food more often than chance in any of the three conditions, instead favoring the container to their left. This result indicates that black and white ruffed lemurs may not be capable of following gaze

Table of Contents

Introduction

Background

What sets humans apart from other species? Human brains have recently been found to be fundamentally different in their organization from the brains of our closest relative in the animal kingdom, chimpanzees; these differences are located almost entirely in regions associated with complex social cognition and language: the anterior cingulate cortex, the frontoinsular cortex, and the left planum temporale (Premack, 2007). These differences indicate that during the time since humans' evolutionary split from the last common ancestor we share with chimpanzees, human brains may have evolved to be reorganized in these particular areas. This reorganization might actually explain humans' development, since this evolutionary split, of the level of mental complexity we now demonstrate. This conclusion makes intuitive sense because humans obviously exhibit a much greater capacity for social behavior and language than other species; we work together to maintain societies with extremely elaborate hierarchies and rules unlike anything yet observed in any other species. However, in recent years cognitive studies have continuously demonstrated that individuals from other species do have some social cognitive abilities previously thought only to be possessed by humans, such as teaching and deception, which require judgment and perspective taking. How are we to interpret these results, in light of our intuitive and now physical evidence that the human mind is unique in these respects?

The human brain has an expansive range of functions, from the relatively simple processes such as the reflex to breathe to the bafflingly complex processes such as the awareness of oneself as an abstract concept. All living creatures are able to respond to their environment in a way which leads us to believe beyond a reasonable doubt that they possess the basest of these lower order functions (i.e. we know flies can feed themselves because we can watch them feed themselves), but whether humans are alone in our abstract thinking and self awareness is much more difficult to assess. Morgan's canon states that a higher order mental process should not be ascribed when a baser process can be ascribed in its stead (Karin-D'arcy, 2005); humans' minds are extremely complex compared to other species, but as we have only experienced our own mental life it is easy to anthropomorphize by ascribing the same level of complexity to other species or even inanimate objects when that complexity is simply not present. An example of this compulsive anthropomorphizing is our reaction to the observation that wild Koshima macaques all learn to wash potatoes in the sea before eating them, which presumably serves to clean as well as season the vegetable. It is easy and exciting to infer that the monkeys learn to wash potatoes from watching their peers experience success from washing their own potatoes, and especially from watching their mothers do it while they are infants, because that is how culture is transmitted in humans. However, there is no actual evidence that the monkeys are using teaching, imitation, or emulation in this situation. Until this evidence is discovered, we have to assume that each monkey learns this behavior for itself accidentally after simply being around the potatoes and the sea for so long, and especially being raised around their mothers handling potatoes around the sea, that they inevitably drop a potato into the sea at some point and experience the positive results for themselves (Gomez, 2004). As psychologist Benet Galef pointed out in his essay "The Question of Animal Culture" (1992), the social learning

explanation is actually very unlikely in this case because the rate of macaques learning this potato washing technique stayed consistently slow even as the number of monkeys that practiced the technique dramatically increased. Social learning of a behavior is expected to increase proportionately with the number of social models of that behavior, so the fact that these macaques were picking up potato washing at the same slow rate whether only a small handful of their peers were practicing the behavior or almost all of them indicates that seeing the behavior happen more often was not helpful toward their learning of it; therefore the learning most likely was not social. Trial and error learning relies on both positive reinforcement and a complete ignorance of the experiences of others (if one in fact has access to understanding others' experiences). Therefore trial and error learning can be said to be distinct from social learning both qualitatively and quantitatively. Even though it is so easy to see aspects of ourselves in others, we have to be careful not to assume such higher order cognition in other species without sufficient evidence refuting a simpler explanation.

One measure that is commonly used to assess a species' mental complexity is its gesture-following ability, or the ability to follow a human's directional gesture (such as a gaze or a point) to choose between potential food sources (Kaminski et al., 2005; Smet & Byrne, 2013; Udell, Dorey, & Wynne, 2008). The high-level explanation of gesture following is that it signifies an animal's recognition of the gesturer's mental state (Miklosi & Soproni, 2006). By this logic, gesture following to find hidden food requires recognition that the gesturer knows where the food is, and that he or she is communicating this knowledge to the subject so that the subject will find the food. Animals that have robustly demonstrated gesture-following ability include dogs and primates (Agnetta, Hare, & Tomasello, 2000; Call et al., 2003; Call, Hare, & Tomasello, 1998; Hare, Call, & Tomasello,1998; Tomasello, 1999; Tomasello et al., 2007), both considered

to be high in social cognition compared to other species. Gesture following is an extremely adaptive behavior for social animals because it allows information to be transmitted silently and subtly. This type of communication could be helpful to animals who hunt in packs, as it could help them coordinate without being noticed by the prey. This strategy could also potentially be helpful to pack animals that are preyed upon, if their method of defense is to hide; a silent gesture may let the rest of the pack know when to hide or when to move hiding places, and especially if survival is dependent on the success of the group (i.e. pack animals as opposed to more solitary animals) then attention to social cues in this situation would be highly adaptive. For humans, who are especially socially complex, paying attention to each other's facial expressions and body language helps us to infer what others are thinking, also called theory of mind. Theory of mind helps us respond to various social situations appropriately and facilitates the positive social interactions that are necessary to each individual's success in survival and reproduction within the structure of human society.

Gesture following facilitates humans' survival and reproduction by improving their social interactions rather than helping them communicate the location of predators or prey. For example, you might see that a child is crying and pointing or looking at a broken toy. Because of these emotional and directional cues, you are able to immediately infer that the child is sad because the toy broke. The faster you understand why the child is upset, the faster you can do your part to rectify the situation. The result is that you are happier, the child is happier, and any bystanders who do not like loud crying noises are happier, and so your community is better able to coexist peacefully. Your survival and reproduction in this case are assisted by your ability to maintain peaceful coexistence with the rest of your community over time rather than immediate consequences on the group's survival.

However, there is also a "low-level" interpretation of gesture following; subjects may be learning how to choose the right location through some kind of visual or spatial cues rather than developing a full representation of the experimenter's intentions (Miklosi & Soproni, 2006). Another possibility is that gesture following is instinctive and not indicative of conscious thought at all. Humans, for example, follow gaze compulsively even when instructed not to (Driver et al., 1999). Another species could potentially have the same instinct to gaze or gesture follow and receive the same benefits without actually understanding the significance of their actions (i.e. finding out about food and danger more efficiently because they reflexively look in the same direction as their peers, not because they actually understand that their peers are looking at the source of food or danger). In a gesture following experiment, species using complex social cognition, such as a human, would reflexively follow the direction of the gesture and still choose correctly based on conscious knowledge that the location being gestured at is likely the correct one, while a species using less complex social cognition might reflexively follow the same gesture and choose based on a directional bias that has now been created. Forming representations of what others are thinking helps humans navigate their complex social structures, but in the context of a gesture following experiment a human's behavior might look identical to that of a species without complex social cognition. The objective of my senior project is to test gaze following ability in black and white ruffed lemurs, and to assess the legitimacy of the gaze following paradigm as an indicator of complex social cognition using this species as a model.

Gesture Following in Animals

Smet and Byrne (2013) found that African elephants can locate hidden food based on a human's pointing gesture. Even though the closely related Asian elephants have not yet been able to demonstrate point following (Plotnik et al., 2013), the African elephants in this Smet and Byrne study were actually able to start using this skill immediately without having to be trained to follow the human pointing gesture, which suggests that they did not have to learn how to follow the cue – at least not in the context of this experiment. In this study an experimenter stood equidistant between two containers and pointed at the baited one. The point itself was static but the experimenter looked back and forth at the elephant and the baited container. Interestingly, these African elephants were able to locate the food correctly at a rate significantly greater than chance even when the human stood closer to the non-baited container and even when he pointed across his body to the container on the opposite side from his pointing arm. The African elephants' responding in the same way to gestures that look different without having to learn the meaning of each new gesture individually suggests that their understanding of (or unconscious response to) the pointing gesture may be a response to an understanding of the intent behind the gesture rather than to the appearance of the gesture. Unless they had learned each of these gestures individually as meaning the same thing before the start of the experiment, the result of this study suggests that the African elephants did not have to learn the gestures because they were able to immediately recognize patterns in the types of gestures the human experimenters were making.

Kaminski et al (2005) found that domestic goats can follow gestures as well. In the first experiment, the experimenter held up food that was visible to one goat but not the other

(prompting the one goat to look towards the food), and coded whether the other goat turned

around to look to the location of the food before the food was thrown down into the goat

enclosure after ten seconds. In the second experiment, the experimenter faced a goat from the

other side of two buckets and indicated which one was baited in one of three ways: a static point

with gaze alternating between the baited bucket and the goat (pointing), a static gaze at the goat

with hand repeatedly touching the baited bucket (touching), and just the gaze alternating between

the baited bucket and the goat (gazing). Goats were able to locate hidden food based on human

pointing to or touching the location, and based on the gaze of another goat that could see the

food, but were not able to use human gaze to find the food. These results imply that there could

be different mechanisms responsible for point following versus gaze following, or that the

adaptive instinct to look at another individual's face might not necessarily influence every

species into looking at the faces of individuals of any other species. Some species may only

instinctively look at the face when viewing conspecifics, perhaps because they do not have an

abstract concept of what a face is which extends beyond the familiar features of their own

species.

Perhaps the most successful species in following human gestures of any kind (besides the

human) is the domestic dog, which has been shown time and again to follow a variety of

different human gestures to find food or targets (Agnetta, Hare, & Tomasello, 2000; Call et al.,

2003; Hare, Call, & Tomasello,1998;Tomasello, 1999). Call et al (2003) found that when

forbidden to approach a piece of food, dogs were sensitive to the experimenter's gaze; however

the experimenter behaved after commanding the dogs to stay away from the food, they were

significantly more likely to approach the food anyway if the experimenter was not actively

watching. If the experimenter turned away, looked away, or even closed his eyes after giving the

command, the dogs were significantly more likely to approach the forbidden food. This interpretation that dogs are sensitive to human gaze was also supported by Hare, Call, and Tomasello (1998), who found that dogs were able to reliably find hidden food from the experimenter's head and eye gaze direction together. However, when the experimenter's head and eye gaze were pointed in different directions, the dogs were not reliably able to locate the food, which suggests that they may have been confused specifically by the experimenter's contradicting body language. Agnetta, Hare, and Tomasello (2000) found that dogs were able to find hidden food from several social cues, including watching the experimenter place a marker in front of the correct location, but were not able to find the hidden food from just the presence of the marker in front of the correct location. This result indicates that dogs' success in gesture following is better attributed to their attention to changes in the human experimenter's behavior (the experimenter placing the marker in front of the correct location) rather than their attention to changes in the environment (the marker simply being in front of the correct location). However, the dogs' inability to extend their understanding of direct human communicative gestures to more indirect forms of communication may indicate that they have only partial understanding of the communicative intent behind the gesture, and make up for this gap in understanding by being extremely attuned to humans' every movement.

Dogs' attunement to human social cues most likely comes from thousands of years of domestication which has specifically selected for those that get along well with humans. Wolves, by comparison, are very closely related to dogs and are even cited by some as being the same species (Agnetta, Hare, & Tomasello, 2000), except that they have not gone through generations of domestication and instead have been hunting with their own kind. Wolves were previously thought to be unable to follow human gestures, but have recently been shown to

follow human points to find hidden food (Udell, Dorey, & Wynne, 2008); in this study hand-reared wolves actually outperformed domestic dogs in following a static finger pointing gesture. However, other similar studies have found captive-raised wolves to follow gestures significantly less often than domestic dogs (Gacsi et al., 2009) or even not at all (Agnetta, Hare, & Tomasello, 2000). If it is the case that wolves are more capable of following an extended-arm pointing gesture than a face and eye turning gesture, the difference may lie in the pointing gesture being a more obvious directional cue to one paying attention to all of its surroundings, while the face and eye gesture is a more obvious directional cue to one paying attention specifically to the experimenter's face; the usefulness of a wolf being able to gesture follow is likely related to wolves' tendency to hunt in packs, in which the location of the prey is likely the most important information to be attuned to. Canines point toward potential prey with their entire bodies rather than just their eyes, so eye-specific information may not be as relevant for wolves. Domestic dogs, on the other hand, need gesture information to mind read; a human's facial orientation may indicate a directional cue, but it may also indicate a number of sentiments and emotions. A dog that can tell the difference between a human looking down because food fell on the floor and a human looking down because he is sad can also tell whether an appropriate response is to look for food or to comfort the human; this dog therefore makes a much better companion than a dog unable to read human social cues, and in turn has a better chance of its survival and reproduction being facilitated by its human companion. Humans are often much more subtle in signaling attention than canines, as we consciously try to stay composed at all times, so in order to make good companions domestic dogs must pay extra attention to changes in their social partners' body language. Because wolves do not rely on pandering to the extreme social complexity of humans for their survival and reproduction, they may pay attention to all their surroundings

rather than focusing intently on humans' faces; therefore wolves might be more likely to notice a large gesture like pointing than a subtle difference in head and eye orientation.

Because humans pay attention to both gazes and points in others, and in fact seem to develop gaze and point following simultaneously under the umbrella of learning joint attention (Brooks & Meltzoff, 2008), one might think that these two types of communicative directional cues would be interchangeable for other species as well. However, although pointing seems obviously communicative to humans, in fact we are unique in the natural extending of our index fingers and therefore also unique in our use of the pointing gesture (Povinelli & Davis, 1994). Chimpanzees and bonobos, both highly social and closely related to humans, are actually much better at choosing the correct baited container when it is gestured to with a flat palm rather than a point and a smile (Herrmann & Tomasello, 2006). Although the authors suggest that this result is due to apes' being better at understanding competitive gestures than cooperative gestures, I believe that the results can also be attributed to the fact that points and smiles are human-specific gestures. Apes have no reason to be attuned to gestures specific to other species, so they were probably confused by them. What is important is not the understanding of the gesture itself, but the understanding of the communicative intent behind the gesture. Given the differences in species' abilities to follow gazes and points and the human-specific nature of points, gaze following seems to be a better paradigm to investigate than point following in non-humans.

Gaze Following in Humans

Humans are incredibly adept at gaze following, an ability which likely is linked to our white scleras that allow us to see each other's eyes very distinctly (see Figure 1). Tomasello et al (2007) found that when an experimenter spontaneously looked up with either his head, his eyes,

or both head and eyes together, human infants respond primarily to eye direction, while other species of ape respond primarily to head direction. Humans are actually born with the ability to follow other humans' head movements (Meltzoff & Brooks, 2007), but by ten to eleven months of age have enough understanding of the significance of the eyes to follow the head movements of people whose eyes are open and not those of people whose eyes are closed (Meltzoff & Brooks, 2007). Around eighteen to nineteen months of age, human babies have developed the ability to use gaze information to find a target (Moore & Corkum, 1998); this ability is distinct from simply noticing changes in gaze like they did before because it requires perspective taking to understand that the gaze is pointed at something in particular as opposed to simply noticing that the experimenter's pupils are moving. Qualitatively this means that older babies can share attention toward a third party location, while a younger infant might just watch a person's head as it moves. This difference may indicate that younger infants do not yet understand that gazing indicates the relevance of a distal point, but it could also have to do with their lack of motor abilities; while they are still unable to locomote, infants' best chance at dealing with a new environmental factor is probably to be connected with an adult who can act to promote their safety and wellbeing.

Humans are actually so good at gaze following that we are unable to stop gaze following. In Driver et al (1999), subjects were primed with photographs of people looking to either the left or the right and were then asked to locate a target which appeared randomly either on the left or the right side of the screen. Even when they were explicitly told that the photograph was not predictive of the target location, and when they were told that the target was four times as likely to be on the opposite side as the gaze, subjects were able to find the target significantly faster

when it was on the same side of the screen at which the gaze was directed. Gazes were eye-only in this study.

Further demonstrating the strength of the human impulse to follow gaze, in Sato, Okada, & Toichi (2007), subjects were primed with drawings and photographs of people looking to either the left or the right and were then asked to locate a target which appeared randomly either on the left or the right side of the screen. Even when the picture was shown so fast that the subjects did not consciously recognize that they had seen a face, the reaction time for finding the target in the same direction that the face was looking was significantly faster than finding a target on the opposite side from the gaze. This effect held with both eye and head gazes, and with eye only gazes where the head is stationary.

The results of these studies suggest that gaze following in humans is due at least in part to reflex, which is consistent with our white scleras (see Figure 1) and gaze following being such a big part of human social interaction. Compared to many other species and specifically to other primates, whose irises and scleras are usually similar in color, humans have a distinct looking eye with small irises contrasted against an elongated white sclera (Kobayashi & Kohshima, 1997).

Figure 1. Chimpanzee eyes compared to human eyes; the contrast between sclera and iris in human eyes makes movements of humans' eyes much more salient than those of chimpanzees' eyes. Image from http://www.nbcnews.com/

These morphological characteristics make the direction in which we are looking especially salient if one looks at our eyes, whereas other species may have better luck from looking at each others' head direction. And while direct eye contact is avoided in many other species for being too confrontational, humans use eye contact to establish social intimacy from when they first open their eyes and through their adult life (Farroni et al, 2002). Human gaze following being due in part to reflex of course does not mean that humans do not understand the significance of gaze following, but rather that they can use unconscious mechanisms to respond to others' gaze changes.

Gaze Following in Apes

Hare et al (2000) found that subordinate chimpanzees only approach food that cannot be seen by a dominant chimpanzee, which suggests that they use gaze information from conspecifics. This finding also supports the high level, social cognition explanation of gaze

following, because the chimpanzees seemed to be incorporating social context into their decision of whether or not to approach the food. In Tomasello et al (2007), an experimenter looked at the ceiling with just his head direction, just his eyes direction, or both. Chimpanzees, gorillas, and bonobos all primarily followed the head direction of the experimenter, spontaneously without a motivation for food, but did not use eye direction information by itself like human infants did in the same circumstances. This result suggests that apes are able to transfer this ability to use gaze information to other species, but that the particular gaze information they pick up on is head orientation rather than eye orientation. In support of these conclusions, Call, Hare, and Tomasello (1998) found that chimpanzees can follow human gazes (head and eyes oriented in the same direction) to find food hidden in one of two containers. Interestingly, the chimpanzees in this study only followed the experimenter's gaze when the experimenter but not the subject had visual access to the contents of the containers during the trial, and not in setups where neither the experimenter nor the subject had visual access inside the containers. This result suggests that the chimpanzees may have been able to consciously reason whether or not the experimenter's gaze information was relevant in any given trial based on whether he could be relied upon to know the location of the food at that time.

Gaze Following in Monkeys

Emery et al (1997) found that when presented with two identical images on opposite sides of a screen, along with a video projection of another monkey facing toward one of the images, rhesus monkeys spend significantly more time looking at the same image that the other monkey also appears to be looking at. Tomasello, Call, and Hare (1998) found several primate species, including sooty mangabeys and three different types of macaques, to all be able to find

food over 80% of the time after a nearby conspecific was induced to turn its head toward the location of the food. These results suggest that monkeys are attentive to the gazes of other monkeys.

The ability of monkeys to transfer their use of gaze information to humans seems to depend on the species. Anderson and Mitchell (1999) found that when a human experimenter spontaneously turns his head to look in a certain direction, macaques also turn to look in the same direction. This result suggests that macaques are able to use gaze information, which in turn suggests that they should be able to find hidden food based on that gaze information. Anderson, Sallaberry, and Barbier (1995) tested capuchins on their ability to find hidden food based on the directional cues of a human experimenter's head and eye gaze, extended hand point, or both gaze and point together. They found that while capuchins were able to find the hidden food based on the pointing gesture information, and based on point and gaze together, gaze information from the head and eyes alone was not enough to help the capuchins find the food. In this sense capuchins may be similar to wolves, which are quite intelligent but lack the sensitivity to social information from faces that dogs and great apes seem to have, in favor of more easily discernible whole-body movements.

Gaze Following in Lemurs

The lemur, a type of prosimian, is thought to have branched off from its last common ancestor with humans and other primates about 60 million years ago (see Figure 2).
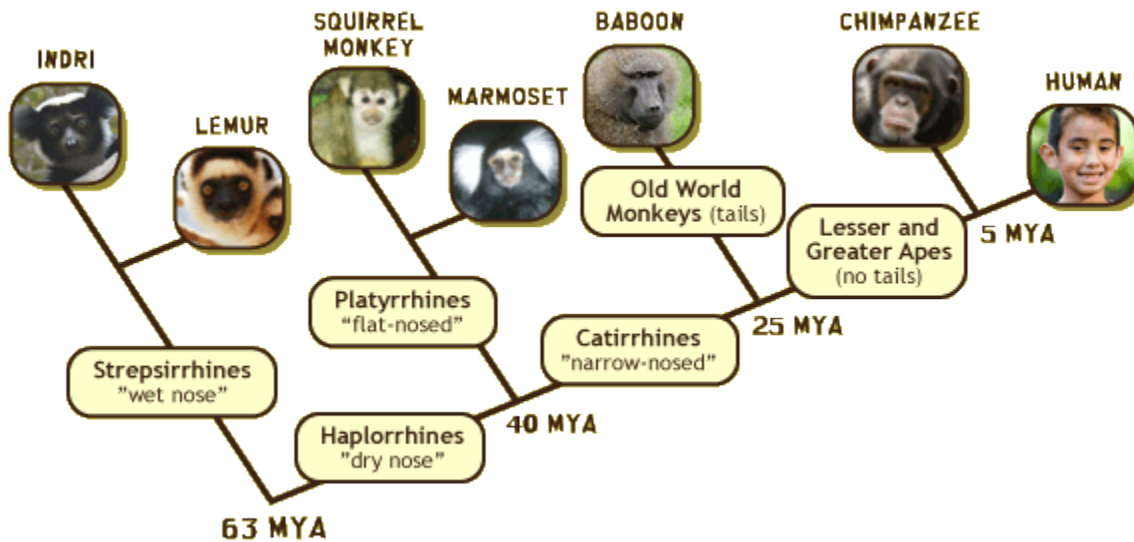
Figure 2. A simplified genealogy tree of primates from http://www.wildexplorations.com/

Lemurs are even more distantly related to humans than new world monkeys and are in fact not even part of the monkey family. Although prosimians are distinct from monkeys in that they are considered to be more primitive, lemurs in particular have exhibited evidence of advanced social cognition comparable to that of more closely related species (Jolly, 1966). Although not as closely related to humans as other great apes, lemurs have demonstrated social learning in using imitation to solve a new task (Stoinski , Drayton, & Price, 2011). In Stoinski, Drayton, and Price's study, black and white ruffed lemurs watched another lemur open an apparatus in one of two ways and were then left alone with the apparatus. All subjects first attempted to open the apparatus in the way that had been demonstrated to them.

Lemurs have been empirically inconsistent in their gaze following behavior. Anderson and Mitchell (1999) attempted a similar spontaneous gaze experiment with lemurs that Tomasello et al (2007) later completed with great apes and human infants as subjects, in which no rewards were available but a human experimenter in front of the subject looked up toward the

ceiling with just his head, just his eyes, or both his head and eyes together. Anderson and

Mitchell found that black lemurs did not follow these spontaneous gaze cues of the human

experimenter, and inferred based on this result that lemurs do not use gaze information at all; if

lemurs could understand the potential significance of gaze changes, why would they willfully

ignore them? However, when food choice was used as a motivator, Botting, Wiper, and

Anderson (2011) found that brown and ring tailed lemurs chose food toward which humans

oriented in their head and body direction, but not eye direction alone. Humans may be distinct in

their ability to follow eye direction alone, as other primates do not have the same white scleras

that make eye direction salient and so they may not have evolved a tendency to pay attention to

each others' eyes. However, these results suggest that lemurs do use at least the face and head

aspect of humans' gaze information when given motivation to do so. The apparent ability of

lemurs to distinguish between relevant and irrelevant situations to gaze follow indicates that

lemurs do not have an automatic impulse to follow gaze – at least not human gaze – in the same

way that humans and other great apes do. Therefore, it is possible that any gaze following they

do exhibit may indicate understanding of the significance of gaze, and potentially even a

conscious decision to follow the gaze information based on evidence that the information is

relevant. Alternatively, selective gaze following may also support a more behaviorist model in

which the lemurs have learned that directional gazes correlate to the location of hidden food

specifically in hidden food tasks, but are not able to transfer this information to understand why a

directional gaze might be relevant outside the context of a game specifically about finding

hidden food. Of course, inconsistent gaze following may also indicate poor experimental design

or only partial understanding of gaze information.

Ruiz et al (2009) found that brown and black lemurs were not able to find hidden food at a rate significantly greater than chance when provided with the directional cue of a photograph of another black or brown lemur facing to either the left or the right (the food was hidden in one of two containers which were directly to the left and right of the lemur, so picking the correct container half of the time was considered to be due to chance). After realizing that the lemurs in this study actually did not look at the photograph stimulus significantly more often than half of the trials, the experimenters reanalyzed their data and found that when they did look at the photograph, these lemurs were able to choose the correct location of the food significantly above chance. This result indicates that lemurs do not look instinctively to the eyes in photographs of faces like humans do, but that they may still be capable of using gaze information from the photographs.

An unfortunate phenomenon in scientific literature is that studies with statistically significant findings are much more likely to be published. The lack of literature regarding gaze following in lemurs may therefore indicate that little research has been conducted on the subject, or alternatively that other research has been conducted but did not produce significant findings. For this reason, replicability of results is crucial to scientific knowledge.

My Study

Lemurs' somewhat inconsistent gaze following behavior seems like it could reasonably fall under either the higher order model of social cognition or the lower order model of directional bias; therefore I want to pit these two possibilities against each other. In order to assess the legitimacy of the gaze following paradigm as an indicator of complex social cognition, I want to test lemurs' gaze following of a live experimenter versus a photograph. Specifically, I

will test the percentage of correct choices lemurs are able to make between two containers, given the cue of a face (live human, photograph of human, or photograph of lemur) gazing in the direction of the container with food inside. I will test the gaze following paradigm particularly with black and white ruffed lemurs, because that is the species that is available for me to work with and has proved to be cooperative with the testing setup. Black and white ruffed lemurs are also interesting in that they appear to be comfortable with many different group sizes, and with splitting up or merging with another group as necessary (Pereira, Seeligson, & Macedonia, 1988). This flexibility of social behavior similar to that shown by chimpanzees may indicate strong social cognitive skills, which makes black and white ruffed lemurs a good candidate for a gaze following study.

Because of the mixed results in previous gaze following studies with lemurs, my first objective is to determine whether this species is in fact capable of gaze following to find hidden food. If the lemurs are capable of gaze following, I expect them to choose the location of the hidden food significantly more often than chance when provided with the directional gaze cue. My second objective, assuming that the lemurs are able to gaze follow in any capacity, is to determine whether their gaze following ability is different in response to a live human face, a photograph of a human face, and a photograph of another lemur's face. The only gaze following study done with lemurs and photographs was with conspecifics in the Ruiz et al (2009) study, so the purpose of the lemur photograph is to try to replicate the results of that study. If gaze following is evidence of advanced social cognition (perspective taking), the lemurs should be more responsive to the live experimenter than the photograph, as the live person is a more reliable social partner responding to the environment as it changes. Whether the lemurs recognize that the live human is actively manipulating the environment versus just responding to

it, does not necessarily alter the explicit usefulness of a live person's social cues in this setup. The photograph, on the other hand, is static and a more indirect social indicator of where the food is, as the social information is in the experimenter's choice of which photograph to put up. Therefore, if the lemur is consciously deciding to take the perspective of the social partner (the experimenter), that social partner's own gaze is the logical next step and a photograph of a third party looking in a certain direction might reasonably give the lemur pause. In support of this interpretation, Troseth, Saylor, and Archer (2006) found that human toddlers follow directions given by a live person much more readily than those given by a video of a person; this result indicates that toddlers recognize live people as being more socially relevant than a 2-dimensional image of a person. If, on the other hand, gaze following is only evidence of directional bias and/or instinctive looking to the face, the lemurs should be equally responsive to the live experimenter and the photograph as the directional stimuli are equivalent. In every condition there is a face in front of the lemur, which is looking in a certain direction. If the lemur simply needs any directional cue to bias its decision, then whether that cue comes from a live face versus an abstract representation of a face should not matter, as long as the face is visible and the directional cue is salient. I am interested in face and eye together gazes in particular because humans seem to be alone in our attention to eye movements, and because various species' inconsistencies between gaze following and point following lead me to believe that gaze following has more potential to be due to social cognition.

One potential confounding factor to watch out for in this experiment is a handedness bias. A familiar phenomenon is the tendency of humans to be right handed, which actually is already present in infancy when most humans choose to lie with their head turned to the right side (Michael, 1981). Right-handedness may actually develop before birth, as ultrasounds have

shown fetuses sucking their right thumbs significantly more often than left as early as fifteen

weeks (Hepper, Shahidulluh, & White, 1991). Surprisingly, Guo, Meints, and Hall (2009) found

that despite humans' tendency to use our right hands over our left hands, we actually also tend to

look to the left side first before the right side when surveying a scene, object, and especially a

face (so the right side of the other person's face is seen first when the viewer and viewee are

positioned directly opposite one another). This study found this leftward gaze bias to also be

present in human infants, rhesus monkeys, and domestic dogs specifically when the subject was

viewing a photograph of an adult human face. These results demonstrate that while we do show

lateral preference in our actions, this lateralization may manifest itself differently depending on

what specific action is being performed or observed. So what about lateralization bias in lemurs

specifically? Similarly to what has been demonstrated in human infants, black and white ruffed

lemurs seem to favor using the hand on the same side as the direction towards which they most

often tilt their head (Nelson et al., 2009). Stafford, Milliken, and Ward (1990) cited a right

handedness bias found in six different species of lemur, including the black and white ruffed

lemur, over various empirical studies. This side bias was especially prominent when the lemurs

were reaching for food, and grew stronger with age. Forsythe et al (1988), on the other hand,

found that five black and white ruffed lemurs favored using their left hands when reaching for

food, especially when the location of the food required the lemurs to drastically reorient their

bodies. When the food was easily reached without reorienting, however, the lemurs showed

much less of a handedness bias. These results suggest that lemurs may default to favoring one

hand over the other, especially in more difficult tasks, but that which hand is preferred may be

dependent on the specific nature of the task. If the lemurs are inclined to use one hand over the

other, then it is likely that one of the containers will be easier for them to reach with that hand.

Therefore, a sign that the lemurs in my study are unable to figure out where the food is hidden based on gaze information may be that they always choose the container on one particular side. If the lemurs do know where the food is hidden, I expect the desire for food reward to outweigh the relative comfort of reaching toward one container over the other.

My first hypothesis is that the black and white ruffed lemurs are capable of gaze following; therefore I predict that they will choose the correct container at a rate significantly greater than chance. If the lemurs are not capable of understanding the directional gaze cues, I would expect them to choose the correct container about half of the time, and possibly to choose the container on one particular side more often than chance. My second hypothesis is that the black and white ruffed lemurs' gaze following is an indicator of complex social cognition; therefore I expect them to choose the correct container significantly more often when the directional gaze cue is coming from a live human experimenter rather than either of the photographs. Because it should be more adaptive for lemurs to be attentive to the social cues of their own kind, I predict that these lemurs may instinctively favor the photograph of the lemur over the photograph of the human. However, because the particular lemurs I am working with have all been raised in captivity and therefore rely on humans for all of their comforts, if gaze following is a product of or at all involves conscious perspective taking, I would expect these lemurs to respond more readily to the live human's gaze than to the gaze of the photograph of the face of another lemur. If, on the other hand, the lemurs have learned to follow human gaze based on visual cues rather than social cues, I would expect them to be more responsive to the gaze of both the live human and the photograph of the human, but less responsive to the photograph of the lemur. So based on my hypothesis that gaze following is due to complex social cognition, I

am predicting the lemurs to gaze follow most consistently with the live human gaze, followed by the photograph of the lemur, and least consistently with the photograph of the human.

Method

Subjects

Subjects were two black and white ruffed lemurs at the Trevor Zoo in Millbrook, NY. Both lemurs were born in captivity. The two lemurs were Fidget, a nine year old female, and Bombo, a two year old male. Fidget had been living solitary for about a year at the beginning of this study, since her previous mate died of old age. Bombo was new to the zoo as of August 2014 and had been living solitary since then at the beginning of this study. Fidget and Bombo began to be introduced in December and were living together in Fidget's main enclosure by the beginning of January. Both lemurs had been previously trained to follow certain procedures, such as daily routines to weigh and feed them, and Fidget in particular had successfully participated in other studies in the past, so both were expected to be amenable to being trained for my study.

Figure 3. Fidget (left) and Bombo (right).

Originally this study included two ring tailed lemurs as well. These were an eleven year old male named Nathan and a twenty-five year old female named Norma. Nathan and Norma shared an enclosure. The two were consistently uncooperative, seemingly not food motivated, and reluctant to separate, so after the training and habituation period they were dropped from the study.

Figure 4. Norma (left) and Nathan (right).

Training and Habituation

Before I began my experiment, I went through a training procedure which was required by the zoo for an outside party to work with their animals. This training covered the handling and diet for the lemurs, as well as what to do in case of a number of emergency situations and how to avoid transmission of zoonotic diseases. My methods were also approved by the zoo administrators as being non-harmful to the animals and as providing them with appropriate, enriching stimulus[i].

Habituation

The first phase was habituation, which ensured that the lemurs were comfortable with each stimulus they would be presented with during testing. To habituate the lemurs to the photograph stimulus, I put one photograph of myself inside each enclosure. The photograph was a life size color image of my head on an 8 ½ by 11 inch piece of paper. Because the directional gaze was meant to be a novel stimulus during testing, the habituation photo was of me looking straight ahead and a bit down so as not to seem threatening.

Figure 5. Stimulus used to habituate lemurs to a photograph of the experimenter

The photograph was laminated and taped to the wall in each exhibit in approximately the expected location that the directional gaze photographs would be placed during testing. I left the photographs in place for six weeks, along with a statement that explained their purpose to the zoo patrons. Every lemur was observed to look at, sniff, or lick the habituation photograph when it was first taped up, and seemed to all be ignoring it by the second week. These observations indicated that the lemurs all successfully noticed and became habituated to the photograph of the experimenter.

Pre-Training

During the time that the habituation photographs were left up in the enclosures, I also trained the lemurs in person once every week to habituate them to the task demands of my study. The goal of this pre-training was for the lemurs to learn the basic setup of the testing – that I had raisins, and that I was hiding the raisins in containers for them to find.

First I isolated the lemur I was training at that moment; during this time the two black and white ruffed lemurs were still being kept in different enclosures so this was not an issue for them. I presented each lemur with the two opaque containers that were later used for testing, on a flat raised surface between me and the lemur I was working with; for the black and white ruffed lemurs I used a large overturned plastic planter or a wooden box as the surface. The containers were each about the size of a mason jar, made of metal and cardboard, with plastic Tupperware-like lids that the lemurs were unable to pry open. I was positioned about a foot behind the containers (which were about a foot away from each other to my right and left), seated, and the lemurs faced me from their seated position on top of the surface and about a half a foot to a foot behind the containers on the opposite side.

Figure 6. Diagram of enclosure and setup used for training and testing.

When the lemurs were too far away I lured them into position by holding out a raisin, and when they got close enough to be on top of the containers I gently pushed them back to about half a foot behind the containers. Once the lemur was in place I first fed it a raisin out of my hand, so that it would recognize that food rewards were available for interacting with me and start to get comfortable with me in general. Then I fed the lemur one raisin out of each container so that it would recognize the containers as a food source. Once the lemurs approached me and the containers to take raisins without running away and needing to be coaxed back, I considered them habituated enough to the various stimuli to begin training.

Each lemur only needed a small handful of pre-training trials on the first day of testing before being ready to move onto the next phase, although Nathan (the male ring tailed lemur) later regressed to the point of refusing to approach me or the containers without running away –

his obstinacy, whether it was due to fear or dislike of me or the activity, was the main reason I

eventually decided to remove him as a subject, and his refusal to be separated calmly from

Norma (the female ring tailed lemur) was the main reason I eventually dropped her from the

subject pool as well.

Training 1

The goal of this first training phase was for the lemurs to learn about the setup of the

experiment in more detail; that one of two containers had a raisin inside while the other was

empty, and that they could choose one container at a time by touching it with their hand. I would

open whichever container they touched first, but not the other one, so if they touched the

container with the raisin inside first they could eat it but if they touched the empty container first

they were not able to eat.

In each trial of this first phase of training, I held out a raisin until I had the lemur's

attention, and then placed the raisin slowly into one of the containers and finally put the lids on

both containers. Because the black and white ruffed lemurs tended to follow the raisin into the

container with their noses, I could be pretty certain that they had seen which container the raisin

went into. However, on the occasional trial in which the lemur did not follow the raisin quite so

closely (and for all the training trials with the ring tailed lemurs who did not get as close), I

would open the container with the raisin inside again and tilt it toward their face, so that the

lemur could see where the raisin was.

After the lemur had seen the raisin in one of the two containers, I closed the lids on both

containers and the lemur could finally choose which container for me to open. A choice was

indicated by the lemur touching one of the containers with one of its hands. If the lemur touched both containers during the designated choosing time in a trial, I would open the first container that the lemur had touched. If the lemur chose incorrectly, then after I showed it the empty container I would retrieve the raisin from the other container and begin the next trial with the same raisin being placed into the same container as in the previous trial.

If a lemur did not touch the containers, I shaped its behavior by first opening the container if they were facing it, then only if they sniffed around it, and finally only if they touched it. This shaping worked very quickly; the black and white ruffed lemurs were highly food motivated so they were quick to participate once they saw that the containers could be opened again. Fidget and Bombo both used their hands to indicate a choice after only a few initial trials, so I began to only accept hand touches rather than nose touches. Before the lemur had made its choice during training I only looked at the lemur and not specifically at either of the containers, except while I was putting the raisin into one. Between trials I reached behind myself to retrieve a new raisin from a bag in my back pocket outside of the lemur's range of vision. Criterion for completing training was met when a lemur touched the correct container at least eight out of ten consecutive trials. For a choice to be marked "correct", the lemur must have seen the raisin being placed into the correct container before choosing, as opposed to not paying attention and making a blind choice which happened to be correct. Any touching of the containers before a raisin has been put into one was not counted as part of the trial and did not result in the container being opened. Where the lemur looked was generally immediately obvious to me in person (as mentioned previously, the black and white ruffed lemurs tended to keep their noses about an inch away from the raisin at all times so it was very easy to tell if they had seen it or not). However, I took a video recording of all training sessions to refer to in case I

was not sure whether a lemur had seen the raisin during a particular trial. The lemur facing the

containers with eyes open as the raisin went in, or as the container was opened again to reveal

the raisin, counted as the lemur having seen the raisin inside of the correct container. Assuming

that the lemurs were all cooperative, each day I did a minimum of ten and a maximum of thirty

pilot trials until the lemurs met criterion. The black and white ruffed lemurs cooperated for at

least the minimum number of trials every time I worked with them, but the ring tailed lemurs

were much more sporadic. Nathan (the male ring tailed lemur) refused to cooperate for ten trials

on any given day, so I continued to train him on this stage as I moved forward with the other

lemurs with the hopes that he would eventually meet criterion. Ultimately, however, I dropped

him from the subject pool once the black and white ruffed lemurs were ready for testing and he

had still not made any progress.

To ensure that the ring tailed lemurs were food motivated, their breakfasts were held until

I was done testing each day. However, the black and white ruffed lemurs were so food

motivated that they had to eat before testing so that they could stay calm enough to focus on the

tasks. I experienced various troubles with the video camera in the first three visits, so I cannot

say for sure which lemurs were able to meet criterion for this phase of training, but definitely by

the fourth week the video records were sorted out and Fidget, Bombo, and Norma could all be

clearly seen to meet criterion in the first ten to fifteen trials.

Training 2

Once the lemurs became comfortable with the training 1 task they all tended to get too

close to the containers or even sit on top of them, and no longer responded to my gently pushing

them back. In order to ensure that the face stimulus would be salient enough to be noticed

during testing, I introduced a new phase of pilot testing which required the lemurs to move back to about half a foot behind the containers at midline before a new raisin would be introduced. I placed a piece of tape down on the platform at this desired midline spot and then put a raisin on top of the tape between trials. This forced them to have their faces at midline when the next trial began. I repeated the procedure of showing the lemurs the raisin as I put it into one of the containers, but in this phase the lemurs had to start behind the containers at midline before the raisin was introduced. Fidget and Bombo reached criterion (eight out of ten consecutive trials) on the first day of this training phase, but after two weeks Norma performed inconsistently and Nathan had still yet to move past the previous training stage, so I finally decided to drop both of the ring tailed lemurs from the subject pool and just focus on the two black and white ruffed lemurs for the remainder of this study.

Testing

Live Gaze Condition

In the "live gaze condition", each lemur was presented with two identical opaque containers placed on a flat surface between the lemur and myself. One container already had a raisin inside but the lemur had not seen the raisin. First I placed a raisin behind the lemur at midline so that it would turn around, and while it was distracted I placed down the containers and turned my head to gaze intently toward the one with the raisin inside. Therefore once the lemur had turned back around to face in my direction the containers as well as the gaze stimulus were already in place. I continued to gaze at the baited container until the lemur placed its hand on one of them (which I could see with my peripheral vision even if they chose incorrectly). Then I opened the chosen container so the lemur could eat the raisin inside or, if it had chosen

incorrectly, see that there was no raisin inside. My face was about a foot away from the

containers, and at the beginning of the trial the lemur was seated about a foot away from the

containers on the opposite side facing me – although once the trial began they tended to get

closer. For a choice to be marked as "correct", the lemur had to have seen the stimulus of my

face before making its decision. Where the lemurs looked was assessed with video recording at

a later time. A lemur facing in the direction of my face with eyes open counted as it having seen

my face. Each visit I did ten trials in the live gaze condition with each of the lemurs,

counterbalanced between the two containers. If a lemur chose incorrectly, after they were

finished inspecting the empty container I replaced its lid and began the next trial by placing a

half raisin behind the lemur at midline and repositioning the two containers using the same bait

raisin as in the previous trial.

Photo Gaze Condition

In the "photo gaze condition", each lemur was presented with the same two containers on

the same platform. First I placed a raisin behind the lemur at midline so that it would turn

around, and while it was distracted I placed down the containers and held up a photograph of

myself looking in the direction of the baited container. The photograph was just of my head, in

color on an 8 ½ by 11 piece of paper, and laminated just like the photograph from habituation.

The only difference is that I was facing down and to one side in the photograph, so as to appear

to be looking at one of the containers[ii]. Because in person my left side looks slightly different

from my right side, to make this stimulus as similar as possible to the live gaze condition I took

two different photographs for the left and right photograph instead of flipping the same

photograph. However, I made sure that the photographs were similar in size, lighting, and visibility of both eyes.

Figure 5. Stimulus used for the photo gaze condition.

I held this photograph in front of my face, obstructing my view of the lemur's face but not of the containers, until the lemur placed its hand on one of the containers. Then I placed the photograph down and opened the container the lemur had chosen so that it could eat the raisin inside or see that there was no raisin inside. For a choice to be marked as "correct", the lemur must have seen the photograph before making its choice. Where the lemurs looked was assessed with video recording at a later time. A lemur facing the photograph with eyes open counted as it having seen the photograph. Each time I visited the zoo I performed ten trials in the photo gaze condition with each of the lemurs, counterbalanced between the two containers.

Conspecific Gaze Condition

In the "conspecific gaze condition", each lemur was presented with the same two containers on the same flat surface as in the other two conditions. I placed a raisin behind the lemur at midline so that it would turn around, and while it was distracted I placed down the containers and held up a photograph of another lemur of the same species looking in the direction of the baited container. The photograph was just of the head of the lemur, in color on an 8 ½ by 11 piece of paper, and laminated just like the photographs from habituation and the photo gaze condition. Similar to the photographs in the photo gaze condition, the lemur in this photograph was facing down and to one side, so as to appear to be looking at one of the containers. In this case I digitally flipped the same photograph for use in both the left and right facing stimuli.

Figure 6. Stimulus used for the conspecific gaze condition.

I held this photograph in front of my face, obstructing my view of the lemur's face but not my view of the containers, until the lemur placed its hand on one of the containers. Then I placed the photograph down and opened the container the lemur had chosen so that it could eat the raisin inside or see that there was no raisin inside. For a choice to be marked as "correct", the lemur must have seen the photograph before making its choice. Where the lemurs looked was assessed with video recording at a later time. A lemur facing the photograph with eyes open counted as it having seen the photograph. The purpose of this condition was to see if I could replicate the results of the Ruiz et al (2009) study, as I am using those results as the basis for my own study and so I need to make sure they are replicable. This condition also provides a control for the possible effect of species difference between the subject and myself; given the differences in morphology and social rearing between humans and captive lemurs, the lemurs may be better able to interpret gaze information from other lemurs than from humans. Each time I visited the zoo I performed ten trials in the conspecific gaze condition with each of the lemurs, counterbalanced between the two containers.

Ordering of Trials

I designed an order of thirty trials that was counterbalanced between the live gaze condition, photo gaze condition, and conspecific gaze condition[iii]. Each condition was presented ten times during this order, with five looking to the left and five looking to the right. The type of stimulus was not repeated more than two trials in a row, and the direction of the stimulus was not repeated more than two trials in a row. I repeated this same order of trials once with every lemur each time I visited the zoo. Between trials I placed a raisin behind the lemur at midline so that it would turn around, and while it was facing away I set up the next arrangement of containers. If

the lemur had gotten the previous trial right I opened both containers, dropped a raisin into one while the lemur was turned around, and then closed both containers before the lemur could see the location of the raisin. If the lemur had gotten the previous trial wrong, I closed the empty container which had been opened, and then while the lemur was facing away I rearranged the two containers into the proper setup for the next trial.

<div style="text-align:center">Results</div>

Reliability Coding

From a total of 720 trials, 400 were reliability coded from the video records (55.6%). The reliability coder (fellow psychology student Grace Shu) checked the condition and direction of the stimulus, which container the lemurs chose, which hand they chose with, and whether they received a reward[iv]. Of the trials that were reliability coded, 98% were in agreement in all categories between the experimenter and the reliability coder.

Overall correctness

The lemurs' overall rate of correctness over a total of 720 trials – 360 trials for each lemur – was almost exactly half (51% correct). A one-sample T-test showed that this value is not significantly greater than chance ($t(23)=0.56$, $p=0.58$). Fidget had a slightly higher percentage of correct choices than Bombo, with 53% of her trials correct as opposed to Bombo's 49% correct, but a 2-sample T-test showed that they did not perform significantly differently from each other overall ($t(22)=1.4$, $p=0.17$)
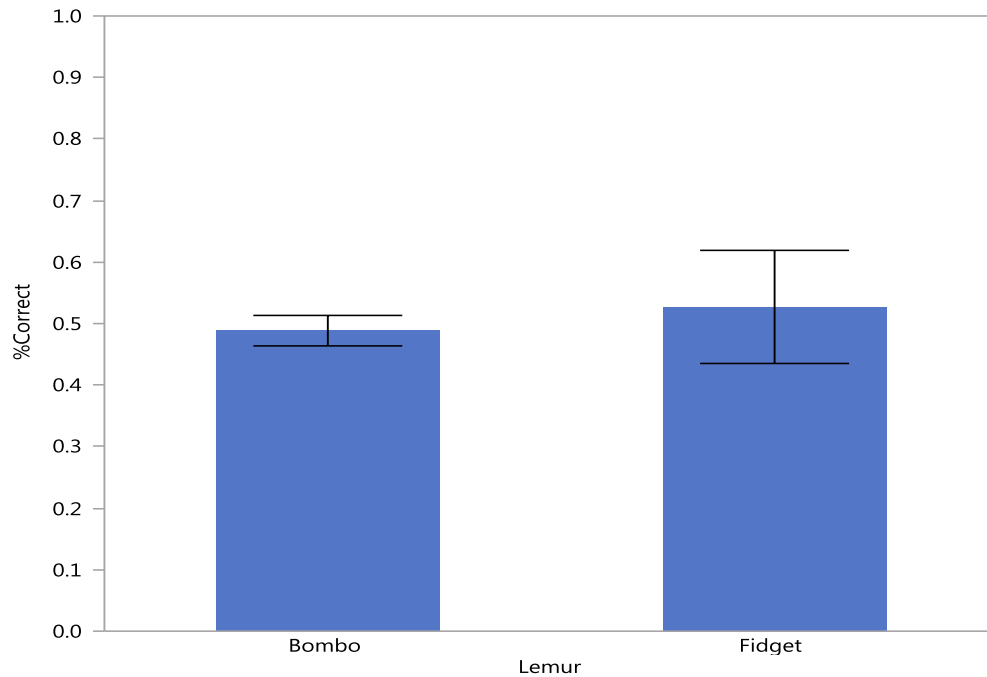
Figure 7. Average per cent correct choices for each lemur. Error bars represent one standard deviation from the mean.

Effect of condition on correctness

A series of one-sample T-tests for the results of both lemurs combined showed that none of the conditions were significantly more likely than chance to result in a correct choice (live gaze $t(23)=0.49$, p=0.63); (conspecific gaze $t(23)=0.77$, p=0.45); (photo gaze $t(23)=0.94$, p=0.36). Numerically – although not significantly – the conspecific gaze condition had the most correct choices (52%), followed by the photo gaze condition (51%), and finally the live gaze condition (49%). Although I considered the possibility of individual differences in the lemurs' success in the three conditions, a 2-way ANOVA showed that there was no interaction effect between which lemur was being tested and the condition on whether the lemurs were able to find the hidden food ($F(2)=1.02$, p=0.6).
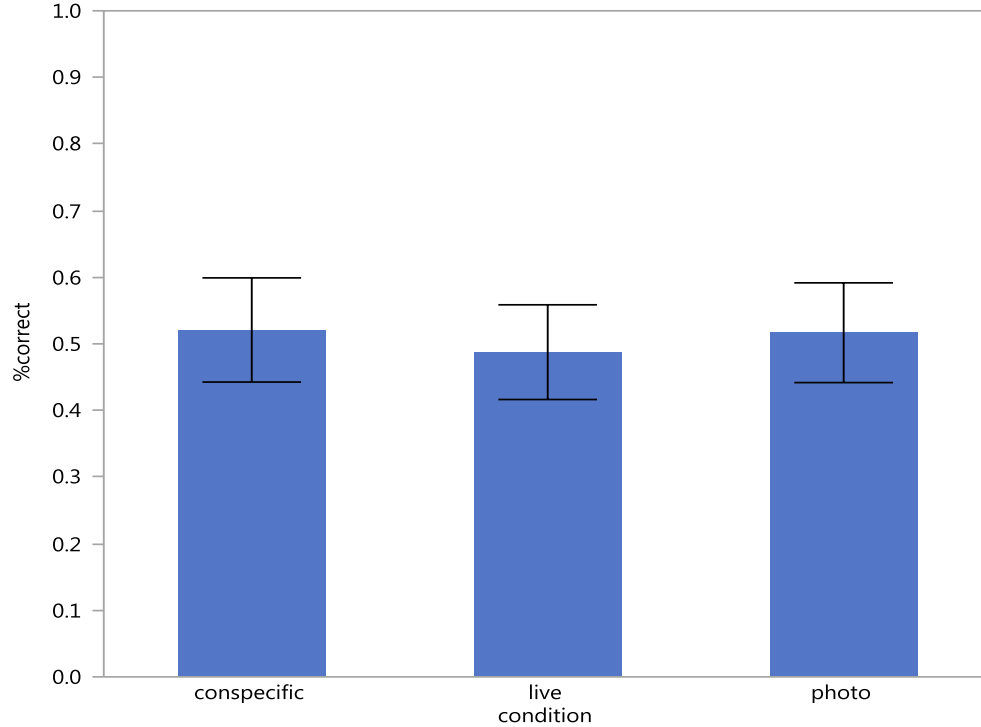
Figure 8. Average per cent correct choices in each condition. Error bars represent one standard deviation from the mean.

Effect of side on correctness

The side of the baited container and cue did have an effect on whether the lemurs were able to find the hidden food.   In trials in which the container to the lemurs' right was baited, the lemurs chose the correct container 23% of the time. In trials in which the container to the lemurs' left was baited, the lemurs chose the correct container 79% of the time. A 2-sample T Test showed that correctness varied significantly between sides ($t(70)$=12.07, p<0.0001).
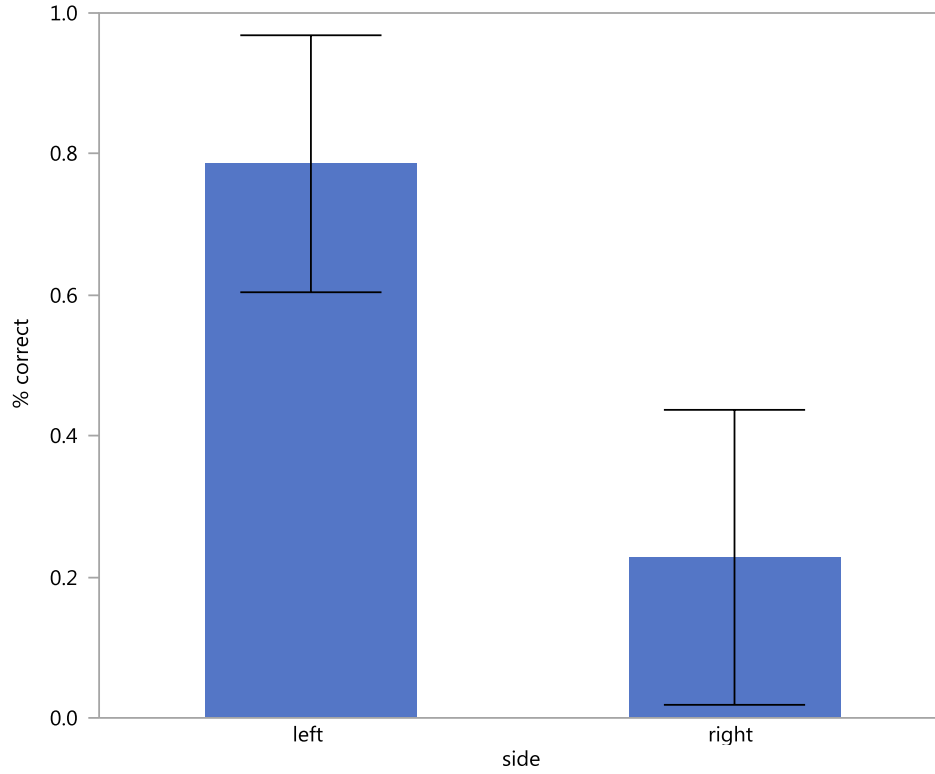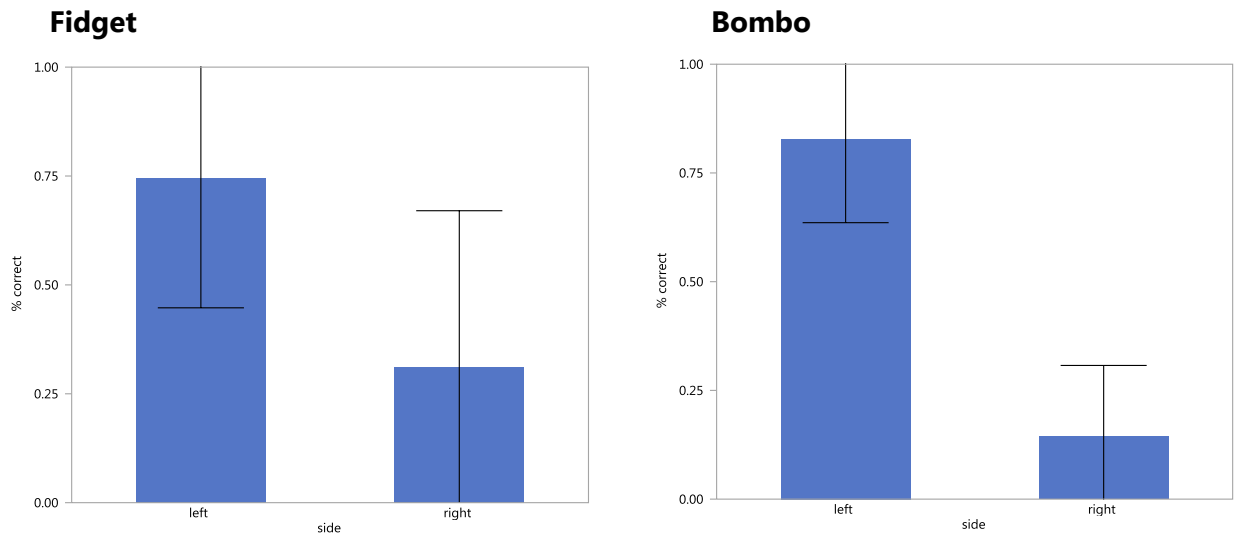
Figure 9. Average per cent correct choices for each side. Note that "left" and "right" refer to the perspective of the lemurs. Error bars represent one standard deviation from the mean.

Figures 9a (left) and 9b (right). Average per cent correct choices for each side, separated by lemur.

Eliminating the variable of correctness from consideration, the lemurs also chose container to their left (with their right hand) overwhelmingly – an overall rate of 78%. A 1-sample T-test showed that this rate is significantly greater than chance (t(23)=5.72, p<0.0001). Bombo chose the container to his left at a rate of 84% (t(11)=9.1, p<0.0001). Fidget chose the container to her left at a lower rate (71%), but a 1-sample T-test showed that even this rate was significantly greater than chance (t(11)=2.44, p=0.03). A 2-sample T-test showed that the two lemurs' handedness biases were not significantly different from each other (t(22)=-1.34, p=0.19). However, another 2-way ANOVA showed that there was an interaction effect between which lemur was being tested and the side of the stimulus on whether the lemurs were able to choose the correct container (F(1)=5.34, p<0.021). Bombo's handedness bias appeared to be much stronger than Fidget's; in the trials with good preserved video records, Bombo used his right hand 99% of the time, and reached across his body 89% of the time. Fidget, on the other hand, used her right hand only 56% of the time, and reached across her body only 64% of the time. This fraction of the total data includes two of the three days that Fidget favored the right side container instead of the left side container, so these percentages are not necessarily a reflection of the lemurs' handedness patterns throughout the study.
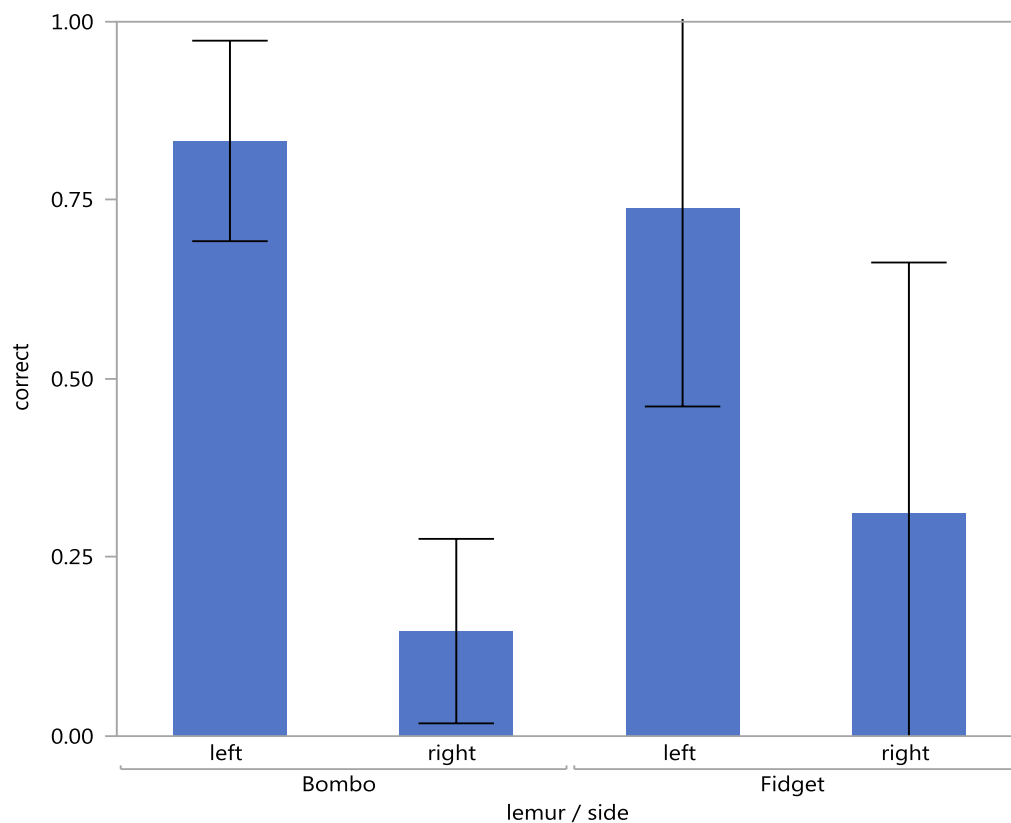
Figure 10. Average per cent correct choices for each lemur on each side. Note that "left" and "right" refer to the perspective of the lemurs. Error bars represent one standard deviation from the mean.

Effect of side vs condition on correctness

A 2-way ANOVA showed that there was no interaction effect between the type of stimulus and the side of the stimulus on whether the lemurs were able to find the hidden food ($F(2)$=3.23, p=0.2), so the lemurs did not have a difference in side bias between the different conditions.
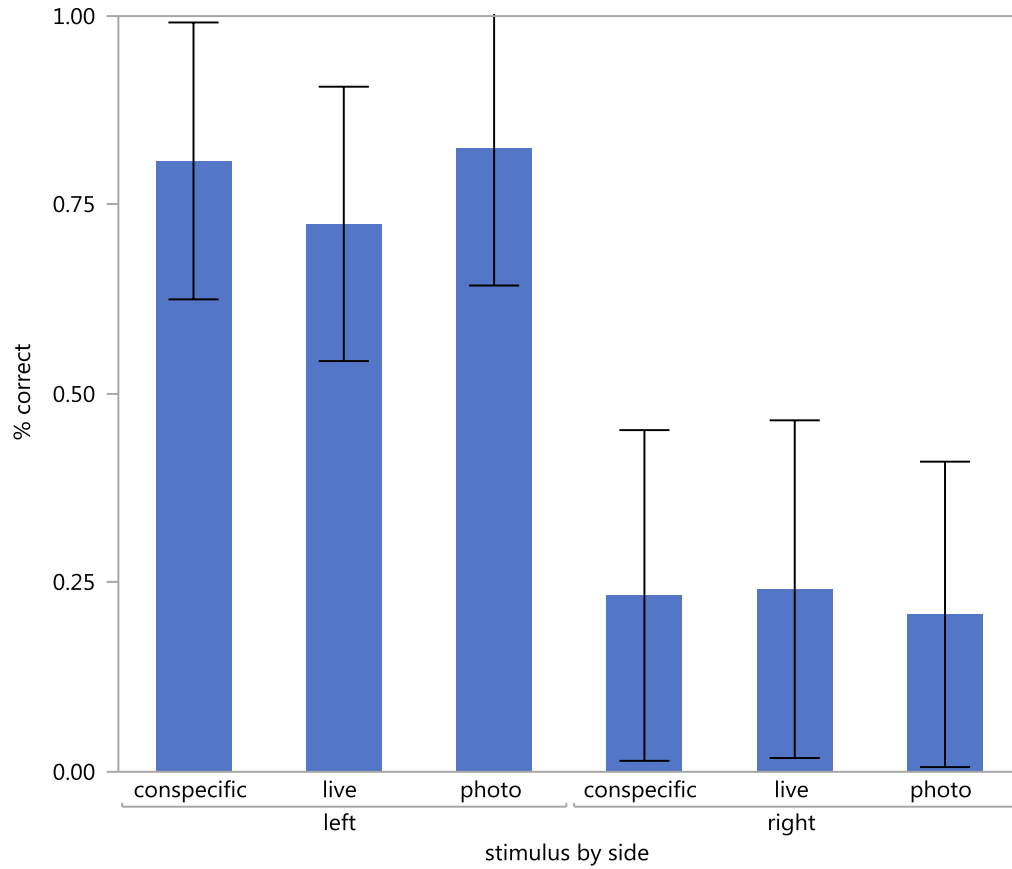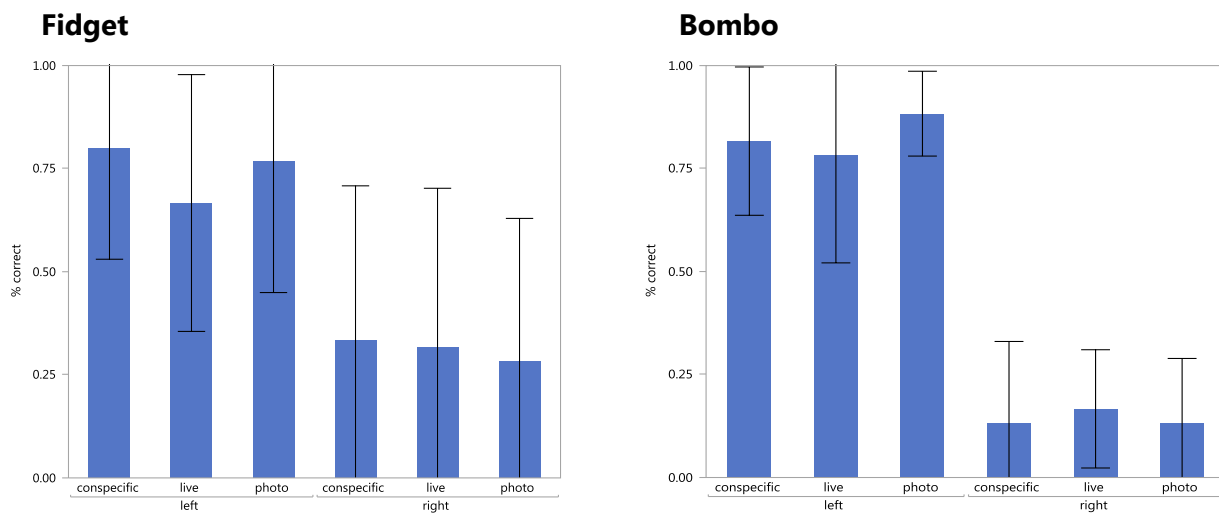
Figure 11. Average per cent correct choices in each stimulus condition on each side. Note that "left" and "right" refer to the perspective of the lemurs. Error bars represent one standard deviation from the mean.

Figures 11a (left) and 11b (right). Average per cent correct choices in each stimulus condition on each side, separated by lemur.

A 2-way ANOVA showed that there was a significant interaction effect between day and the side of the stimulus on the lemurs' ability to find the hidden food ($F(11)=116.19$, $p<0.0001$); toward the end of the testing period the lemurs had more of a side bias, with a slight dip on the very last day (figure 8).
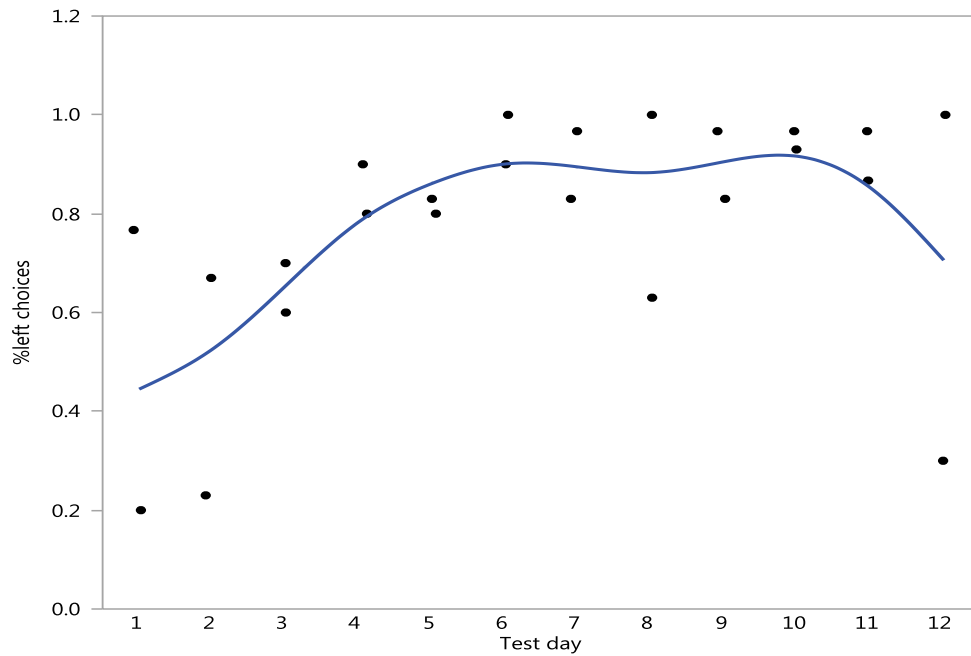

Figure 12. Per cent of trials in which the left side container is chosen for each testing day. Note that "left" refers to the perspective of the lemurs.

Fidget
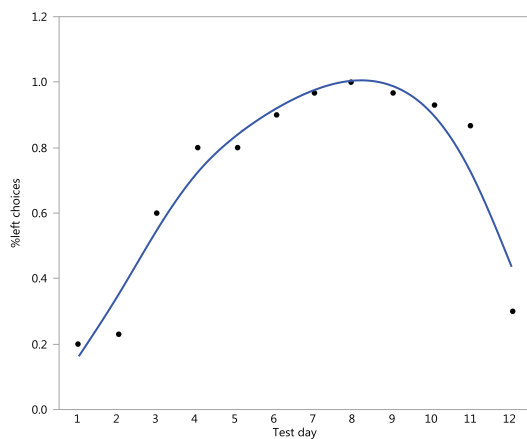
Bombo
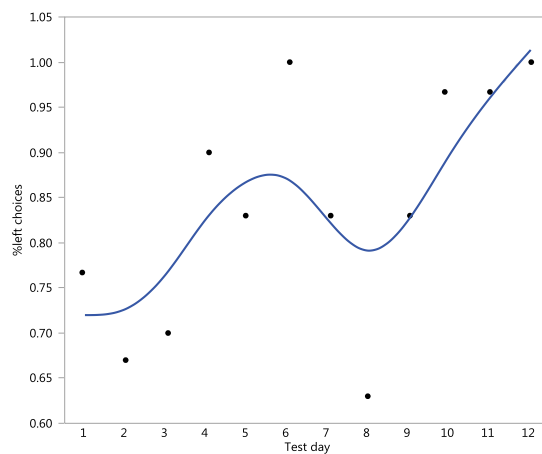
Figures 12a (left) and 12b (right). Per cent of trials in which the left side container is chosen for each testing day, separated by lemur.

Effect of time on correctness

A 2-way ANOVA showed a significant interaction effect between day and trial number on whether the lemurs chose correctly ($F(319)=394.3$, p=0.0025), although neither effect was significant on its own (day $F(11)=13.92$, p=0.24); (trial $F(29)=18.81$, p=0.93); some days the lemurs made more correct choices at the beginning of the trial period, and some days they made more correct choices at the end of the trial period (figure 13).
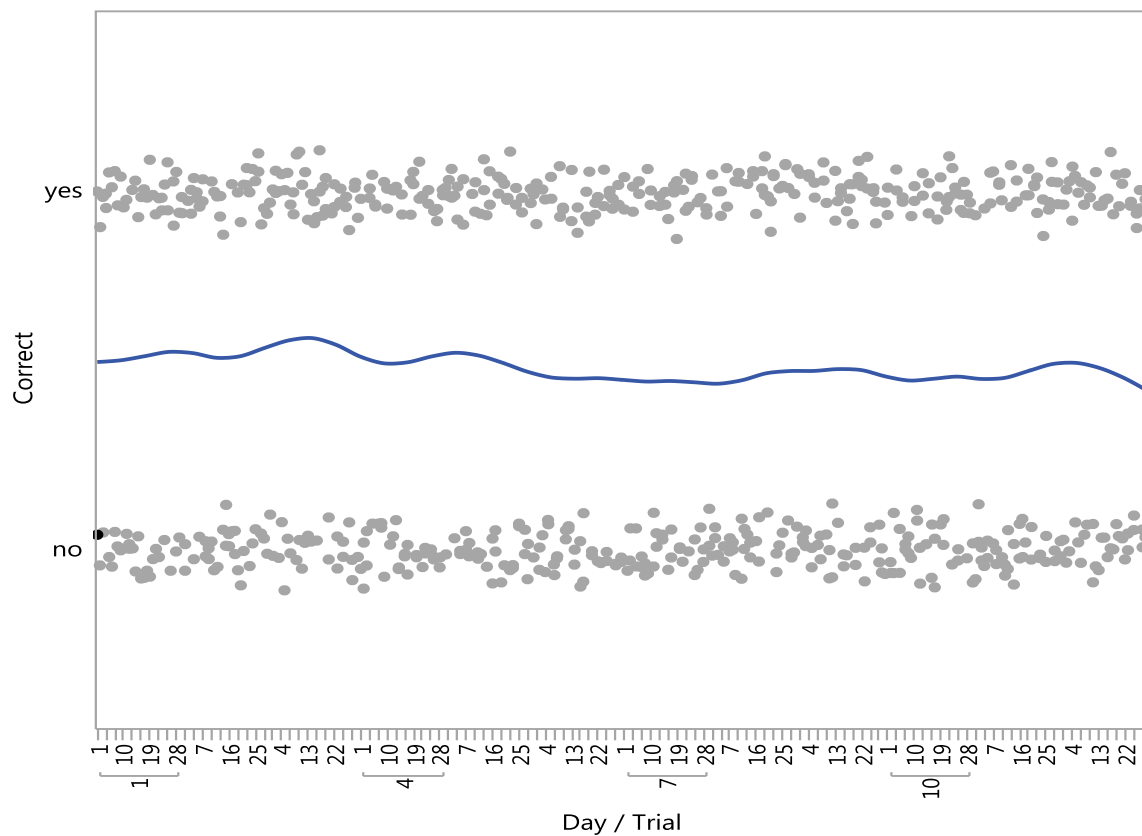
Figure 13. Trend line follows the number of correct versus incorrect choices over each consecutive trial during the testing period: 30 trials per day for 12 days for a total of 360 trials per lemur.

Fidget   **Bombo**
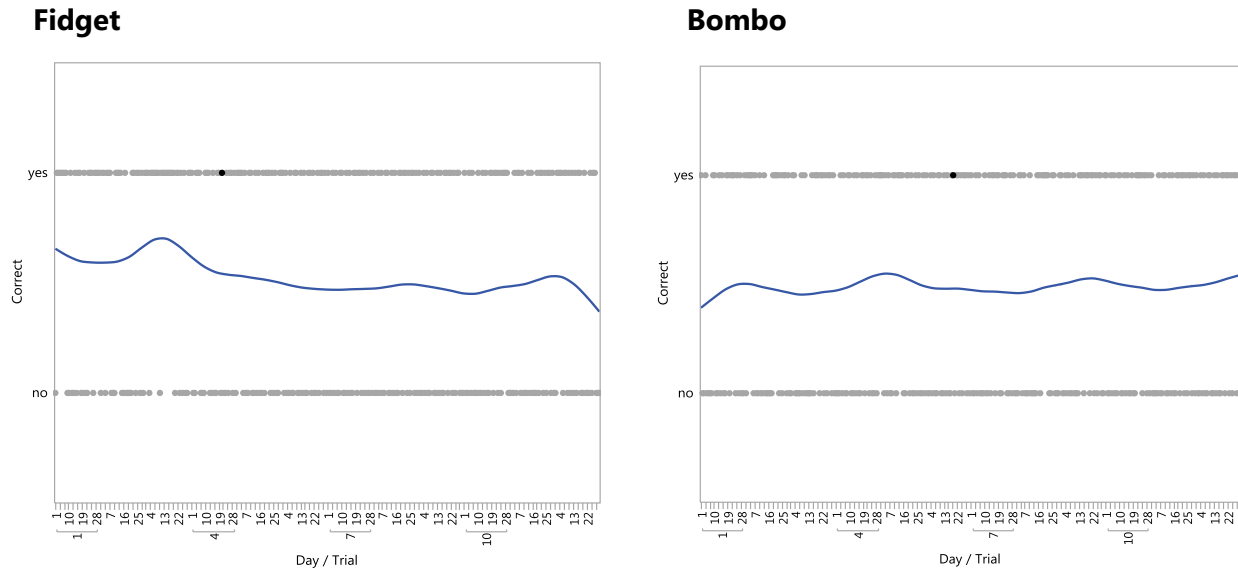
Figures 13a (left) and 13b (right). Trend line follows the number of correct versus incorrect choices made by each lemur over each consecutive trial during the testing period: 30 trials per day for 12 days for a total of 360 trials each.

Discussion

Hypotheses

My hypotheses were that black and white ruffed lemurs are capable of gaze following, and that this gaze following is an indicator of social cognition. Therefore I was expecting that the lemurs would be able to reliably find the hidden food given the stimulus of a face looking at its location. I was also expecting a difference in the lemurs' gaze following ability to the three different types of stimuli (live human face, photo of a human face, photo of a lemur face) which would give insight into whether lemurs' gaze following is a function of social cognition or some other method. The lemurs being more responsive to the live gaze stimulus would support a social cognition explanation, because the social information presented from a person turning her

head is much simpler than the information presented from her holding up a picture of herself turning. The two scenarios are visually congruent, though, so if the lemurs were not using social cognition I expected them to perform similarly with the live gaze condition and the photograph gaze conditions.

Interpretation

Neither of my hypotheses were supported by the results of this study. Neither lemur reliably used the gaze cues of any of the three face stimuli to find the hidden food at a rate greater than chance, at any point during testing. In contrast, when they saw which container the food went into during training they consistently chose correctly at least eighty per cent of the time. Because the lemurs did not successfully gaze follow in any of the conditions, I did not have anything meaningful to compare that might tell me how gaze following works. Therefore if lemurs are in fact capable of gaze following, I have no new information that would indicate whether or not this ability is due to social cognition.

Instead of choosing the containers based on the gaze cues or even directional cues, in the absence of direct cues to the reward's whereabouts the lemurs both consistently chose the container to their left (except for three days in which Fidget preferentially chose the container to her right instead). When they actually watched me hide the raisin in training trials, however, the lemurs reached for the correct container at least 80% of the time without fail – even at the end of February when I returned to a set of training trials to make sure the lemurs were still trained to the task demands. The lemurs' consistent success in the training trials indicates that their side bias does not outweigh their desire for food. Their success in the training trials, especially those in February, also indicates that they knew to tap the container they expected to find food inside

of. The fact that the lemurs almost always reached left during testing, in contrast to their success during training, suggests that they did not understand the gaze cues, and so in the absence of indication to where the food was hidden they reverted to a side bias.

My interpretation that the lemurs understood the task demands that were introduced to them during training brings up the obvious question of why they would even choose incorrectly up to 20% of the time if they knew how to find the food. I chose the threshold of 80% because that is well above chance and seemed to be used often in other studies. I believe this discrepancy can be attributed in part to the subjects occasionally losing focus, which could have caused them to either not see where I put the raisin or to forget where they had seen me put it. I was certainly aware of various environmental factors that could be distracting, such as noise coming from the other lemur, people passing through the zoo, and the parrots across the hall.

The 2-way ANOVA significant interaction effect of lemur and side on correctness, as well as the significant interaction effect of side and day on correctness, can be explained by Fidget switching her side preference to the right for three days while Bombo consistently favored the left (Bombo chose the left side container 84% of the time while Fidget only chose the left container 71% of the time – both significantly more often than chance but still moderately different from each other). I'm not sure why Fidget changed her preference around, or why either lemur deviated from their side biases at all during testing. It is possible that the lemurs did not rely solely on handedness due to another false understanding of the task demands; in the absence of understanding the gaze stimuli, it is possible that the lemurs tried out a few different unsuccessful strategies before settling into the quick and moderately effective system of choosing the same container almost every single time. This interpretation is supported by the

increase in same side choices over time – Bombo started out choosing the left side container about 72% of the time, and by the last day of testing he was choosing the left side container nearly 100% of the time. Fidget spent three days choosing mostly the right container, but on any given day was choosing the same side container about 90% of the time.

I initially thought the 2-way ANOVA significant interaction effect of day and trial on correctness might indicate that the lemurs began to learn the order of where the food was being hidden as the testing period went on. However, figures 13a, 13b, and 13c clearly show that there was not a trend of improvement over time but rather some days happened to go better or worse than others. This result, then, could also support the interpretation that the lemurs sometimes tried other methods out that were even less reliable than chance before settling on choosing the same container every trial. Figures 13b and 13c show that the lemurs' success varies over the course of the testing period; this variation could of course be due to chance, but it could also further support the interpretation that the lemurs varied their approaches toward trying to find the hidden food.

Implications

Not finding gaze following in two lemurs does not by any means warrant the conclusion that lemurs are not capable of gaze following; it could indicate that these lemurs in particular are not capable of gaze following, or that my methods were flawed in some way. However, my results have caused me to view the previous literature on lemur social cognition with more skepticism. For instance, consider the contrast between the lemurs in Anderson & Mitchell (1999) who failed to follow spontaneous gaze changes with the lemurs in Botting, Wiper, & Anderson (2011) who were able to find hidden food when gaze information was provided. Why

would lemurs only follow gaze when they know food is available but not when the consequences are unknown? The whole benefit of gaze following is that it allows one to access information that another individual is aware of. Choosing to follow gaze only when you know there's a reward in it for you seems to negate the whole element of learning new information, like the appearance of danger or a new food source. It is certainly possible that the lemurs in both studies were capable of following gaze but only used the skill when motivated by a known food reward, but it is also possible that the lemurs in Botting, Wiper, & Anderson (2011) were finding the food some other way (perhaps by smelling it). Consider too the lemurs in Ruiz et al (2009), who were able to find hidden food based on the gaze cues of a photograph of another lemur only when they looked at the stimulus, but who did not even look at the gaze stimulus in more than half of the trials. If the lemurs were able to find food using information from the gaze stimulus that was placed right in front of their faces, why did they not start paying more attention to it? Instead they only used the stimulus when they happened to look right at it, which seemed to only be by accident. Seeing Fidget and Bombo's eagerness to get food as fast as they could, the results of these studies do not bode well for the prognosis of gaze following being a function of social cognition.

An interesting issue is the standard of success in comparative cognition studies. Many researchers consider a species to understand a concept if they can use it to solve a problem at least 80% of the time, or even if they can use it significantly more often than chance. I would expect a human with full understanding of gaze information to be able to find the hidden food 100% of the time without fail, so why do we allow for another species to getting 20% of their tasks wrong? When a lemur watches me place a raisin into one of two containers, why would it

then choose the opposite container? I think a great deal of this is that we cannot have direct communication with the animals. For instance a human subject would be able to articulate that they weren't paying attention, or needed to start over or take a break, whereas if this is the case for a nonhuman the trial still goes on and is coded as if the individual does not grasp the concept in question. This may also indicate, however, that the individual's grasp of the concept is shaky and so while this concept may bias their responses they still do not have a full understanding of what is going on.

There is currently very little literature available on the subject of gaze following in lemurs. A very important part of the scientific process, however, is being able to replicate results. One of my objectives in this study was to replicate the results of the Ruiz et al (1999) study, in which lemurs were able to find hidden food when they first looked at a photograph of another lemur facing toward the food's location. Similarly to the lemurs in this past study, my subjects were not able to find the food more often than chance overall. However, although the stimulus was positioned in plain sight right in front of the lemurs' faces, I was not able to tell from my video records whether the lemurs actually made a point to look at the stimulus before making their choices. Therefore I was not able to replicate the result that acknowledging the stimulus increases the lemurs' ability to find the hidden food. The lemurs in the Botting, Wiper, and Anderson (2011) study, on the other hand, were able to find the hidden food when the gaze stimulus was provided even though the experimenters did not check whether they looked directly at the stimulus or not. Even in the live gaze condition my subjects were not able to find the hidden food more often than chance, so I definitely cannot claim to have replicated the results of this past study. The fact that what little information we do have about lemurs' gaze following

ability seems to point in all different directions indicates that a lot more research needs to be done before any conclusions can be reached.

Limitations

One of the main limitations of this study was that I had an extremely small number of subjects, made even smaller by the two ring tailed lemurs being uncooperative and ultimately having to be dropped from the subject pool. While both lemurs showed a bias of using their right hand to reach for the left container, this bias was stronger and more consistent in Bombo. The difference in side bias between the two remaining subjects indicates that while neither lemur understood the gaze following task, the way in which they misunderstood the task was not identical. Therefore I believe it is very likely that more subjects would yield even more variation in technique. The possibility remains that black and white ruffed lemurs as a species are capable of gaze following, even though these two individuals are not, so a larger subject pool would also provide results much more easily generalized to the whole population.

The small sample size also prevented me from investigating differences in gaze following ability between different species of lemur. Even though I had to drop the ring tailed lemurs from the subject pool due to their stubbornness, it is certainly possible that they are capable of gaze following but just chose not to cooperate with me. In fact, on the first day that I came in to the zoo to start training the lemurs, Nathan (the male ring tailed lemur) was actually the most cooperative of the four. While the black and white ruffed lemurs were very aggressive about trying to get to the food, Nathan would watch me hide the raisins from afar and then cautiously step forward and tap the correct container. Because his choices had seemed so calculated, I was very surprised and disappointed to find that he was never once cooperative after that first day.

The zoo staff suggested that Norma (the female ring tailed lemur) had been giving Nathan a hard time for getting so many treats from me when she got none. When I was in the enclosure with both of them together she would often chase him away so that she could interact with me herself, even though she was terrible at training and never even figured out that she was supposed to use her hands. A couple of times when I was actually able to coax Nathan into choosing a container, he startled when he actually saw the raisin inside and ran away to hide from me. It is very possible that Nathan would have been a fine subject otherwise, but that he actually got conditioned by Norma to not cooperate with me.

Another limitation was that these two lemurs in particular were never settled into their environments and were often anxious and distracted much of the time during the testing period. Bombo was new to the zoo, first completely solitary and then shuffled around between different enclosures and introduced to a somewhat unfriendly partner. Fidget had been living in her enclosure for several years, and was used to getting her way – she had been living there alone for a couple years, and for several years before that with a very old and passive partner. She was put on birth control right as I was finishing up training, and was immediately given a new roommate who was much more confrontational than her previous partner. Side effects of hormonal changes from starting or stopping birth control last at least for several weeks in humans (Rosenberg, Meyers, & Roy, 1999), so the case is likely similar for other species. Fidget, however, was only given a few days to recover from her implantation surgery before being introduced to Bombo. My impression from interacting with her during this whole process was that the birth control made her hungrier, and that the presence of Bombo made her more territorial about food. She became much more aggressive about trying to find the hidden raisins,

and even feeding her right before working with her did not seem to remedy this. By the end of the testing period, the lemurs were living together in Fidget's original enclosure but had to be separated for feeding because they were prone to fight over food. This fighting over food had actually increased since they were first put together, and sometimes they would fight even when there was no food around. Both lemurs were consistently uncomfortable with their surroundings and with each other, and this discomfort may have made them feel like it was more important to act quickly toward finding food than to actually figure out how to find it. Therefore, it is possible that if the experiment were to be repeated in a few months once they are both settled in they would have more brain power to devote to figuring out where I was hiding the raisins and may even show indications of gaze following.

I had a lot of trouble with my video recordings during the course of this study. Because of how curious and hands-on the black and white ruffed lemurs tend to be I had to leave the camera outside their enclosure, which also means that I was not able to monitor it during the recordings and only found out later if there was a problem. Many of my videos are out of focus and do not capture the lemurs' eyes. Therefore I was not able to check whether the lemurs actually looked at the stimulus before choosing a container – the defining variable in the Ruiz et al (2009) study – and so I am not sure if my results replicate this study or not. I have a few partial videos from the camera switching off on its own in the middle of a recording. Having another person present to handle the camera would have helped with these problems. However, I also accidentally deleted several of my videos from the computer in an effort to clear disk space. I didn't lose any data from this incident because I always live coded every trial, but because of the lost video records I was only able to have about 56% of the trials reliability coded. This

reliability coding had a 98% agreement rate on which stimulus was used, which container was chosen, and whether a reward was given, but there is still the possibility that I live coded more trials incorrectly that were not able to be reliability coded.

It is also possible that the lemurs did not have enough motivation to figure out how to find the hidden raisins for my experiment. There was no penalty for a wrong choice, because there were so many trials in a row and no matter what the lemurs got half a raisin in between trials to place them at midline behind the containers. In fact it may have been a more fruitful strategy for the lemurs to choose quickly with a 50% success rate than to figure out how to find the hidden raisin more reliably, because the quicker they made any decision the quicker more raisins would be available. I setup the experiment to have the lemurs receiving a lot of raisins very quickly because whenever I took too long to get set up they seemed to get frustrated and became uncooperative. Other studies, like the Ruiz et al (2009) study, had a more controlled testing environment that did not allow for the lemurs to come and go as they pleased. This controlled setup allowed the denial of rewards for wrong choices to have more impact, because the subjects could not simply leave when they were no longer interested in the activity. These other studies also had more time to test their subjects, so they were able to throw out and repeat any trials in which any potential distractions were present. My subjects were always potentially distracted by being able to smell and hear, but not see, the other. It is possible that they would have eventually put in the mental effort to figure out that they were supposed to be following gaze if I had been more patient in working with them, or if I had a more controlled testing environment.

An obvious limitation of this study was that the subjects were not able to perform the desired task (gaze following) despite some previous studies indicating that they could, so I did not actually have a chance to meaningfully compare their performance in this task between the different stimulus conditions. This study ended up functioning as more of a blanket gaze following experiment, investigating whether black and white ruffed lemurs could follow gaze information to find hidden food (and concluding that they cannot). My lack of findings may be due to the species' inability to gaze follow, but it could also be because of some error in my methods. Another possibility is that black and white ruffed lemurs do possess gaze following ability as a species, but for some reason these two individuals do not.

Future Directions

Another effort to replicate the Ruiz et al (2009) study would be helpful. This could mean actually capturing on camera whether the lemurs looked at the stimulus or not before making their choice as I had originally intended to do before failing so spectacularly at keeping good video records. A more fruitful approach, though, might be to train the lemurs to touch the stimulus before they could choose between the two containers, or to place the stimulus in front of the containers, so that they are somehow forced to acknowledge the gaze stimulus in every single trial. This type of setup would slow the lemurs down considerably, and also eliminate the possibility of having to throw out most of the trials on the basis of the lemurs not looking at the stimulus.

It is certainly possible that performing this same experiment at another time when both subjects are more comfortable with each other and with their surroundings, and therefore less anxious about food, would yield more accurate results. Even better, though, would be to find a

larger sample of black and white ruffed lemurs. This could be accomplished by visiting several different zoos, or possibly even a sanctuary, and would help to control for the effect of these individual differences.

Another complement to my study, which I definitely would have done if I had more time, would be to test the lemurs with some other types of directional cues that did not involve gaze like pointing to, touching, or placing a marker over the correct container. If the lemurs were able to use these cues but not gaze cues, this result (especially in conjunction with the results of the Ruiz et al (2009) study) might indicate that they are able to take directional cues from their environment but do not seek for them from social partners. If they failed to use these additional directional cues, on the other hand, that result might indicate that black and white ruffed lemurs in particular are too anxious to get at the food to pay close attention to all features of their surroundings. In that case another setup which forces the subjects to observe the setup before acting might be appropriate and yield better results.

Accepting the possibility that lemurs might simply not be capable of gaze following, this same study would be helpful to try out on another species that definitely can follow gaze – like chimpanzees or domestic dogs – for actual insight into the possible mechanisms behind gaze following. Troseth, Saylor, and Archer (2006) showed that human toddlers take social information much more readily from a live person than from a video of a person, but we already know humans use complex social cognition and this type of live versus image comparison is severely lacking in other species. Comparing results between different species might give some good insight as well, if they derive social information from different cues. For example, maybe some species would only be able to follow the gaze of conspecifics, indicating that they may be

paying attention to a certain visual cue that defines their own species. Cotton top tamarins, for instance, are much more likely to co-orient with a conspecific than with a human experimenter (Neiworth et al., 2002), as are domestic goats (Kaminski et al., 2005). Another type of animal might only be able to follow the gaze of a live social partner, which could indicate that they rely on sensory information other than vision for social information so a 2D representation of a face is not a sufficient cue.

One of the assumptions I was working under during this study is that an individual who understands the social significance of gaze following would respond differently to different types of gaze stimuli. An important next step would be to see if this is actually the case in a species who definitely understands gaze following: humans. We already know that toddlers are more attentive to direction from a live adult than to a video of an adult (Troseth, Saylor, & Archer, 2006), but this study was not about gaze following specifically. It is certainly possible that humans – especially older humans – are so good at gaze following that the source of the gaze information does not make a difference in our gaze following ability; for instance, we may be just as willing to follow the gaze of a photograph of a hippo as a live human. Instead of simply coding "correct" versus "incorrect", maybe a different measure like response time would be more appropriate for the dependent variable in this type of study.

Conclusion

Going into this study I had a lot of optimism about lemurs' gaze following ability and social prowess. This optimism only increased as I trained Fidget and Bombo, who both quickly caught onto the task demands and seemed eager to play along. In contrast to my expectations, however, the lemurs did not exhibit any gaze following ability toward me or toward either of the

two types of photographs and instead consistently chose the container to their left. Therefore, I was unfortunately not able to investigate the mechanisms behind gaze following ability. I cannot say for sure whether these lemurs' failure to follow gaze in my study represents an inability of the species as a whole, an inability of these particular lemurs, or some fault in my own methods. There certainly were a lot of issues that came up in my methodology; I only had two subjects, the lemurs were not yet comfortable with their new living situation, and it was not obvious that they ever took the time to notice the stimulus in their frantic search for food. However, my personal impression is that both of my subjects are healthy, intelligent lemurs who were confident in their understanding of my experiment (though this understanding was misguided). Therefore my personal interpretation of my results is that they represent an inability of lemurs – at least of black and white ruffed lemurs – to use gaze information in locating hidden food. In retrospect, the studies I previously cited as indicating that lemurs are capable of gaze following seem a bit more suspect. For example, the fact that the lemurs in the Ruiz et al (2009) study only used the head-and-eye gaze stimulus when they happened to look right at it rather than actively seeking it out, even though it was right in front of them, no longer seems like a clever discretion in deciding which social information to use. Instead I believe that if they were even using gaze information at all in this study, rather than their results being some kind of anomaly, it was purely because of a directional bias that was created when they accidentally looked at the face stimulus. The results of my study support this interpretation that lemurs lack the social cognition necessary to reliably follow gaze.

References

Agnetta, B., Hare, B., & Tomasello, M. (2000). Cues to food location that domestic dogs (Canis familiaris) of different ages do and do not use. *Animal Cognition*, 3: 107-112.

Anderson, J. & Mitchell, R. (1999). Macaques but not lemurs co-orient visually with humans. *Folia Primatol*, 70: 17-22.

Anderson, J., Salisberry, P., & Barbier, H. (1995). Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour*, 49(1): 201-208.

Botting, J., Wiper, M., &Anderson, J. (2011). Brown (Eulemer fulvus) and ring-tailed lemurs (Lemur catta) use human head orientation as a cue to gaze direction in a food choice task. *Folia Promatol*, 82:165-176.

Brooks, R. & Meltzoff, A. (2008). Infant gaze following and pointing predict accelerated vocabulary growth through two years of age: a longitudinal, growth curve modeling study. *Child Language*, 35: 207-220.

Call, J., Hare, B., & Tomasello, M. (1998). Chimpanzee gaze following in an object-choice task. *Animal Cognition*, 1: 89-99.

Call J., Brauer, J., Kaminski, J., & Tomasello, M. (2003). Domestic dogs (Canis familiaris) are sensitive to the attentional state of humans. *Journal of Comparative Psychology*, 117: 257-263.

Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition*, 6(5): 509-540.

Emery, N., Lorincz, E., Perrett, D., Oram, M., & Baker, C. (1997). Gaze following and joint attention in rhesus monkeys (Macaca mulatta). *Journal of Comparative Psychology*, 111(3): 286-293.

Farroni, T., Csibra, G., Simion, F., & Johnson, M. (2002). Eye contact detection in humans from birth. *PNAS*, 99(14): 9602-9605.

Forsythe, C., Milliken, G., Stafford, D., & Ward, J. (1988). Posturally related variations in the hand preferences of the ruffed lemur (Varecia variegata variegata). *Journal of Comparative Psychology*, 102(3): 248-250.

Gacsi M, Gyori B, Viranyi Z, Kubinyi E, Range F, Belenyi B, & Miklosi A. 2009. Explaining dog wolf differences in utilizing human pointing gestures: selection for synergistic shift in the development of some social skills. PLoS ONE, 4: e6584.

Galef, B. (1992). The question of animal culture. *Human Nature*, 3(2): 157-178.

Gomez, J. C. (2004). Social learning, imitation, and culture. In *Apes, Monkeys, Children, and the Growth of Mind* (pp. 238-265). Cambridge, Massachusetts and London, England: Harvard University Press.

Guo, K., Meints, K., & Hall, C. (2009). Left gaze bias in humans, rhesus monkeys and domestic dogs. *Animal Cognition*, 12: 409-418.

Hare, B., Call, J., & Tomasello, M. (1998). Communication of food location between human and dog (Canis familiaris). *Evolution of Communication*, 2(1): 137-159.

Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59: 771-785.

Hepper, P., Shahidulluh, S., & White, R. (1991). Handedness in the human fetus. *Neuropsychologia*, 29(11): 1107-1111.

Herrmann, E. &Tomasello, M. (2006). Apes' and children's understanding of cooperative and competitive motives in a communicative situation. *Developmental Science*, 9(5): 518-529.

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science*, 153(3735): 501-506.

Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, Capra hircus, follow gaze direction and use social cues in an object choice task. *Animal Behaviour*, 69(1): 11-18.

Karin-D'Arcy, M. (2005). The modern role of Morgan's canon in comparative psychology. *International Journal of Comparative Psychology, 18*: 179-201

Kobayashi, H. & Kohshima, S. (1997). Unique morphology of the human eye. *Nature*, 387: 767-768.

Meltzoff, A. & Brooks, R. (2007). Eyes wide shut: the importance of eyes in infant gaze-following and understanding other minds. In R. Flom, K. Lee, & D. Muir (Eds.), *Gaze following: Its development and significance* (pp. 217-241). Mahwah, NJ: Erlbaum.

Michael, G. (1981). Right-handedness: a consequence of infant supine head-orientation preference? *Science*, 212(4495): 685-687.

Miklosi, A. & Soproni, K. (2006). A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*, 9: 81-93.

Moore, C. & Corkum, V. (1998). Infant gaze based on eye direction. *British Journal of Developmental Psychology*, 16(4): 495-503.

Neiworth, J., Burman, M., Basile, B., & Lickteig, M. (2002). Use of experimenter-given cues in visual co-orienting and in an object-choice task by a new world monkey species, cotton top tamarins (Saguinus oedipus). *Journal of Comparative Psychology*, 116(1): 3-11.

Nelson, E., O'Karma, J., Ruperti, F., & Novak, M. (2009). Laterality in semi-free-ranging black and white ruffed lemurs (Varecia variegata variegata): head-tilt correlates with hand use during feeding. *American Journal of Primatology*, 71(12): 1032-1040.

Pereira, M., Seeligson, M., & Macedonia, J. (1988). The behavioral repertoire of the black-and-white ruffed lemur, Varecia variegata variegata (primates: lemuridae). *Folia Primatologica*, 51(1): 1-32.

Plotnik, J. et al. (2013). Visual cues given by humans are not sufficient for Asian elephants (Elephas maximus) to find hidden food. *PLoS ONE*, 8(4): e61174.

Povinelli, D. & Davis, D. (1994). Differences between chimpanzees (Pan troglodytes) and humans (Homo sapiens) in the resting state of the index finger: implications for pointing. *Journal of Comparative Psychology*, 108(2): 134-139.

Premack, D. (2007). Human and animal cognition: continuity and discontinuity. *PNAS,* 104(35): 13861-13867

Rosenberg, M., Meyers, A., & Roy, V. (1999). Efficacy, cycle control, and side effects of low- and lower-dose oral contraceptives: a randomized trial of 20 μg and 35 μg estrogen preparations. *Contraception*, 60(6): 321-329.

Ruiz, A., Gomez, J., Roeder, J., & Byrne, R. (2009). Gaze following and gaze priming in lemurs. *Animal Cognition*, 12: 427-434.

Sato, W., Okada, T., & Toichi, M. (2007). Attentional shift by gaze is triggered without awareness. *Experimental Brain Research*, 183(1): 87-94.

Smet, A. & Byrne, R. (2013). African elephants can use human pointing cues to find hidden food. *Current Biology*, 23(20): 2033-2037.

Stafford, D., Milliken, G., & Ward, J. (1990). Lateral bias in feeding and brachiation in Hylobates. *Primates*, 31(3): 407-414.

Stoinski, T., Drayton, L., & Price, E. (2011). Evidence of social learning in black-and-white ruffed lemurs (Varencia variegata). *Biology Letters*, 7(3): 376-379.

Tomasello M. 1999. Domestic dogs (Canis familiaris) use human and conspecific social cues to locate hidden food. Journal of Comparative Psychology, 113: 173-177.

Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: the cooperative eye hypothesis. *Journal of Human Evolution*, 52(3): 314-320.

Troseth, G., Saylor, M., & Archer, A. (2006). Young children's use of video as a source of socially relevant information. *Child Development*, 77(3): 786-799.

Udell, M., Dorey, N., & Wynne, C. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour,* 76(6): 1767-1773. doi:10.1016/j.anbehav.2008.07.028

Appendix

MILLBROOK SCHOOL

Trevor Zoo

ACCREDITED BY THE
ASSOCIATION OF ZOOS & AQUARIUMS

The faculty of the Millbrook School Science Department and the Trevor Zoo believe that independent research can be an excellent educational experience. We encourage students of all ages to consider the use of the Trevor Zoo collection for appropriate non-invasive behavioral studies.

The Trevor Zoo maintains and regularly reviews an animal use policy that governs all research on the zoo's collection. Students who wish to conduct research at the zoo must complete the application on the reverse of this document.

Proposals will be evaluated by the Director, Director of Programs, and Animal Care Coordinator of the Trevor Zoo and may be approved, approved with modifications, or rejected. All approved projects must be supervised by a member of the zoo staff. Appropriate citation of the Trevor Zoo must be included in any publication or presentation of experiments conducted at the zoo.

Finally, it is considered a privilege to be able to conduct research at a zoological institution and the opportunity requires that each student must demonstrate respect for their subjects and the research program. Failure to do so will result in termination of the project.

If you are interested in conducting research at Millbrook School's Trevor Zoo involving live animals, please complete the application on the back of this page and submit it to:

Dr. Alan Tousignant

Trevor Zoo at Millbrook School

131 Millbrook School Road

Millbrook, NY   12545

Phone: 845-677-3704

Please note that for proposals from outside of the Millbrook School community there is a non-refundable administrative and training fee of $40.00. Checks may be made out to Trevor Zoo.

Trevor Zoo Research Proposal

Principal investigator: Hannah Mason   Date: 9/3/14

Brief description of proposed experiment (one or two paragraphs):

Lemurs have been shown to gaze follow; given the choice between two containers that may contain food, lemurs will opt for the one that the experimenter is staring at. To investigate whether this phenomenon can be attributed to conscious thought or to a reflex like directional bias, I will compare lemurs' success in following the gaze of a live experimenter (me) versus the gaze of a picture of a person.

First I will habituate the lemurs to my presence, the presence of the picture, and to the concept of choosing between two containers for a possible food reward. For testing I will isolate the lemur in question and present it with the two containers, and either gaze myself at the one with food in it or present a photograph of a person gazing at the one with food in it. Once the lemur has reached for one of the containers I will open it and give the lemur its contents: either a snack or nothing. I will also include a condition in which the picture and I are looking at different containers, both of which contain food. I am interested in how fast the lemurs learn to gaze follow with the live experimenter versus the picture, and which stimulus they prefer when both are available.

Animal requirements:

Species involved: black and white ruffed lemur and ring tailed lemur
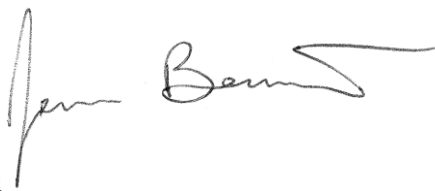
Number of specimens: 4

Are there any special needs? I want to use food as reward, and I would like to test the lemurs individually

Time of day experiment will be conducted: Wednesday mornings

Duration of experiment (for completion of experiment): testing ends in February (6 months) but the project is due in early May (8 months)

Application received:

Zoo staff decision: Approved

Staff supervisor: Jessica Bennett, Director of Programs

Training Data Sheet

Date:

Lemur ID:

Trial #	Choice Correct? (Y/N)	Sees raisin before choice? (Y/N)

Live Testing Data Sheet

Date:

Trial #	Trial Type	Bombo (correct y/n)	Fidget (correct y/n)
1	Live Gaze – Right		
2	Conspecific Gaze – Left		
3	Photo Gaze – Left		
4	Photo Gaze – Right		
5	Live Gaze – Left		
6	Conspecific Gaze – Right		
7	Conspecific Gaze – Left		
8	Photo Gaze – Left		
9	Live Gaze – Right		
10	Photo Gaze – Right		
11	Conspecific Gaze – Left		
12	Live Gaze – Left		
13	Live Gaze – Right		
14	Photo Gaze – Left		
15	Conspecific Gaze – Right		
16	Conspecific Gaze - Left		
17	Live Gaze – Left		
18	Photo Gaze – Right		
19	Live Gaze – Right		
20	Conspecific Gaze – Left		
21	Photo Gaze – Right		
22	Conspecific Gaze – Right		
23	Live Gaze – Left		
24	Photo Gaze – Right		
25	Photo Gaze – Left		
26	Conspecific Gaze – Right		
27	Live Gaze – Right		
28	Photo Gaze – Left		
29	Conspecific Gaze – Right		
30	Live Gaze – Left		

Figure iv. Testing data sheet with predetermined order of trials. Since we are sitting opposite each other, "Right" refers to my right and the lemur's left, while "Left" refers to my left and the lemur's right.

Name of Reliability Coder: Date:

Date of Testing:

Lemur ID (circle one):   Fidget   Bombo

Left and Right are from the perspective of the lemur, not the experimenter. Please note whether I held up the correct stimulus based on this chart, which container the lemur touched, which hand it touched the container with, and whether the choice was correct. I know these videos are a little confusing, and you may find the audio helpful as I tried to narrate the trials while they were happening, but I understand that you may need to leave a good amount of these spaces blank.

Trial	Trial Type		Container (L/R)	Hand (L/R)	Correct (Y/N)
1	Live Gaze – Left				
2	Conspecific Gaze – Right				
3	Photo Gaze – Right				
4	Photo Gaze – Left				
5	Live Gaze – Right				
6	Conspecific Gaze – Left				
7	Conspecific Gaze – Right				
8	Photo Gaze – Right				
9	Live Gaze – Left				
10	Photo Gaze – Left				
11	Conspecific Gaze – Right				
12	Live Gaze – Right				
13	Live Gaze – Left				
14	Photo Gaze – Right				
15	Conspecific Gaze – Left				
16	Conspecific Gaze – Right				
17	Live Gaze – Right				
18	Photo Gaze – Left				
19	Live Gaze – Left				
20	Conspecific Gaze – Right				
21	Photo Gaze – Left				
22	Conspecific Gaze – Left				
23	Live Gaze – Right				
24	Photo Gaze – Left				
25	Photo Gaze – Right				
26	Conspecific Gaze – Left				
27	Live Gaze – Left				
28	Photo Gaze – Right				
29	Conspecific Gaze – Left				
30	Live Gaze – Right				