Journal of Comparative Psychology
2013, Vol. 127, No. 1, 82–90

In the public domain
DOI: 10.1037/a0027261

The Effect of Body Orientation on Judgments of Human Visual Attention in Western Lowland Gorillas (*Gorilla gorilla gorilla*)

Amanda E. Bania and Erin E. Stromberg
Smithsonian's National Zoological Park, Washington, DC

The ability to appreciate the attentional states of others is an important element used in discerning the presence of Theory of Mind in an individual. Whether primates are able to recognize attention, and further, use such information to predict behavior, remains contentious. In this study, six western lowland gorillas (*Gorilla gorilla gorilla*) were tested under different conditions that aimed to investigate not only their understanding of what a human experimenter sees, but also what information they use to make these judgments. In all experiments the gorillas selected between two human experimenters, one who could see them and one who could not. In Experiment 1 the gorillas' performance was significantly above chance in conditions where they judged body orientation, head orientation, and eyes. Experiment 2 showed that the gorillas' initial judgments of attention may be based on body orientation rather than facial cues. Experiment 3 demonstrated that the gorillas were better able to utilize facial cues in some conditions, when these cues were paired with a more neutral body orientation. These findings suggest that the gorillas are using a hierarchical approach to determining visual attention, by making an immediate decision based on the most salient cue—body orientation. However, when body orientation is more ambiguous their ability to judge the less prominent cues of the face and eyes does improve.

Keywords: visual attention, perspective taking, theory of mind, eye gaze, gorilla

Since Premack and Woodruff (1978) first posed the question "Does the chimpanzee have a theory of mind?" numerous studies have been conducted with nonhuman primates, specifically great apes, in an effort to find a definitive answer. Theory of Mind is generally defined as the ability to attribute mental states to others, including an awareness of their knowledge, attention, perception, intentions, and beliefs. To date, experiments designed to explore these abilities have produced mixed results (see Call & Tomasello, 2008 for extensive review). Currently there is little consensus among comparative psychologists as to how these conflicting results should be interpreted, making the subject of nonhuman primate Theory of Mind a topic of continual debate (Andrews, 2005; Penn & Povinelli, 2007; Povinelli & Vonk, 2003; Tomasello, Call, & Hare, 2003).

Although the study of Theory of Mind in great apes has focused on multiple domains, such as gaze following, perspective taking, understanding intention, and knowledge of false beliefs, the mostly widely examined is visual attention. These visual attention studies center on apes' knowledge of perception and attention by exploring not only their understanding of what another sees, but also their recognition of how that is likely to affect an experimenter's (or conspecific's) actions.

Povinelli and Eddy (1996b) conducted a series of experiments with juvenile chimpanzees in an attempt to determine if the chimpanzees had an understanding of visual perception and what information they were using, if any, to make such a determination. In each experiment the chimpanzees requested a food item from either a human experimenter who could see them or one who could not. The authors proposed two theoretical frameworks to evaluate the chimpanzees' performance in these tasks. The mentalistic framework suggested that subjects do understand visual perception and appreciate the connection between eye orientation and the psychological state of seeing. Alternatively, the behaviorist framework posits that subjects do not understand that vision has an associated mental component, but may be able to make associations and learn rules about visual attention through trial-and-error learning, resulting in improved performance over time.

When presented with various nonseeing conditions, the chimpanzees only chose correctly in a condition in which one experimenter was oriented toward the subject and the other was oriented away (front/back). In all other conditions, in which both experimenters were oriented forward and one occluded her face and/or eyes in some way, the chimpanzees performed at chance level (Povinelli & Eddy, 1996b). However, further testing showed that the subjects' performance could improve over time (Povinelli & Eddy, 1996b; Reaux, Theall, & Povinelli, 1999), leading the authors to suggest that the chimpanzees may be using perceptually based rules to determine attention. These findings lend support to the behaviorist framework.

Bulloch, Boysen, and Furlong (2008) tested a different group of highly enculturated chimpanzees and found that they performed

This article was published Online First March 5, 2012.

Amanda E. Bania and Erin E. Stromberg, Center for Animal Care Sciences, Smithsonian's National Zoological Park.

We thank the keeper staff of the National Zoological Park Great Ape House, as well as Lisa Stevens, for their support of this project. We also thank Dr. Marietta Dindo for her valuable comments during the preparation of this article and Dr. Chikako King for her guidance in statistical analysis.

Correspondence concerning this article should be addressed to Amanda E. Bania, Smithsonian's National Zoological Park, P.O. Box 37012, MRC 5507, Washington, DC 20013-7012. E-mail: baniaa@si.edu

well above chance levels under similar conditions (adapted from Povinelli & Eddy, 1996b and Reaux et al., 1999). The chimpanzees were able to reliably select the correct experimenter and did so without the extensive training and testing that the Povinelli and Eddy (1996b) subjects underwent. Their ability to discriminate between seeing and nonseeing experimenters from the first presentation of the condition offers strength to the mentalistic framework and challenges Povinelli's assumptions of chimpanzees' comprehension of visual attention, at least at the species level.

Additional studies in the area of great ape visual attention report varied results but seem to share one commonality, which is that apes are able to respond appropriately to the body orientation of a human experimenter as it relates to attention (Hostetter, Cantero, & Hopkins, 2001; Hostetter, Russel, Freeman, & Hopkins, 2007; Kaminski, Call, & Tomasello, 2004; Poss, Kuhar, Stoinski, & Hopkins, 2006). Some may struggle with appreciating the specific role that the eyes play in visual perception (Kaminski et al., 2004; Theall & Povinelli, 1999), whereas others do seem to demonstrate comprehension (Hostetter et al., 2001; Hostetter et al., 2007; Leavens, Hostetter, Wesley, & Hopkins, 2004; Poss et al., 2006; Povinelli & Eddy, 1996a). These results are more consistent with the mentalistic framework that suggests that apes do have some knowledge of visual perception and can flexibly apply this knowledge to others.

What we know of these abilities in gorillas specifically, comes from a small number studies. Overall, gorillas behave in ways that indicate they have some knowledge of the link between one's eyes and their attention. They have been shown to recruit the help of a human, by first establishing eye contact before indicating a request (Gomez, 1991) and will also increase their use of manual gestures when a human experimenter is oriented toward them rather than away (Poss et al., 2006). Gorillas readily move their location in order to position themselves in front of a person before requesting food, but in other circumstances they directed gestures to a food reward rather than the experimenter (Liebal, Pika, Call, & Tomasello, 2004).

Given the conflicting results of current visual attention studies in apes and the underrepresentation of gorillas in the available literature, our goal was to further explore visual attention and perception in captive gorillas using Povinelli and Eddy's (1996b) classic paradigm and to expand on what is known of their abilities in the area of Theory of Mind.

General Methods

Subjects

Six western lowland gorillas (*Gorilla gorilla gorilla*) housed at the Smithsonian's National Zoological Park in Washington, DC, participated in this study. Subjects included three male (Kojo, 7 years old; Kwame, 9 years old; Baraka, 17 years old) and three female (Kigali, 15 years old; Mandara, 27 years old; Haloko, 42 years old) gorillas. All of the gorillas were members of one stable social group housed in a large indoor enclosure equipped with climbing structures, nesting material and daily novel enrichment items. Access to a large naturalistic outdoor yard was also given during the day as weather permitted. The gorillas' daily diet consisted of a variety of fresh produce, browse, and primate chow, and at no time during the study was access to food or water restricted. All testing occurred when the subjects were individually separated in conjunction with their daily shifting routine. Each gorilla had participated to varying degrees in previous cognitive tasks although their experience is quite limited (Babitz, 2000; King, 2012; Shillito, Gallup, & Beck, 1999; Swartz and Estocsin, 2006). All subjects participated in all of the experiments described in this study.

Pretest

Pretest trials were conducted before the start of Experiment 1. The aims of the pretest trials were to ensure the gorillas were gesturing reliably as well as to identify any existing side or experimenter biases. Such pretest trials were unique to this study and were added because of the limited experience the gorillas had with manual cognitive testing. They offered no opportunity for learning or advantage in the experimental trials. Subjects each received two pretest sessions consisting of eight trials each. During these trials two experimenters (E1 and E2) stood side by side, approximately 90 cm apart, in the adjacent keeper area oriented toward the subject. Subjects were in their primary enclosure separated from experimenters by mesh caging. Facility design was such that the gorillas' enclosure is 0.6 to 0.9 m higher than the keeper area, such that a standing human and a sitting gorilla are at eye-level. The position of the experimenters (left/right) was randomized and counter-balanced within each session. For all pretest trials, both E1 and E2 had visual access to the subject. Each experimenter simultaneously presented a 3-ounce cup of sugar-free gelatin to the subject with her outside hand. The gorillas then had to request food from one of the experimenters by gesturing toward them. During all trials, the experimenters established eye contact with the subject upon presentation and maintained it until a gesture was made. The criterion for gesturing was the extension of a finger, fingers, or hand through the cage mesh discretely indicating one of the two experimenters. Each gorilla was required to complete a minimum of one session in which they met the gesturing criterion in eight of eight trials. Two subjects required additional sessions to establish adequate and consistent gesturing that fell within the defined criterion (Haloko, three sessions total; Baraka, five sessions total).

Experiment 1

Procedure

Experiment 1 consisted of two sets of six sessions, each containing eight trials. Modeled after Reaux et al. (1999), each session presented one of six conditions in which one experimenter was attentive to and making eye contact with the subject and the second experimenter's visual attention was obscured or obstructed in some way, preventing eye contact (see Figure 1). Sessions were organized into two sets; A (Sessions 1–6) and B (Sessions 7–12). Set A was identical to Set B in order of presentation and randomization of trials. This presentation allowed for later analysis of learning effect and general comparison of performance over time. In Condition 1, *front/back*, one experimenter was oriented forward toward the subject, and the other was oriented away from the subject. In Condition 2, *buckets*, both experimenters were oriented forward and one placed a bucket over her head and the other

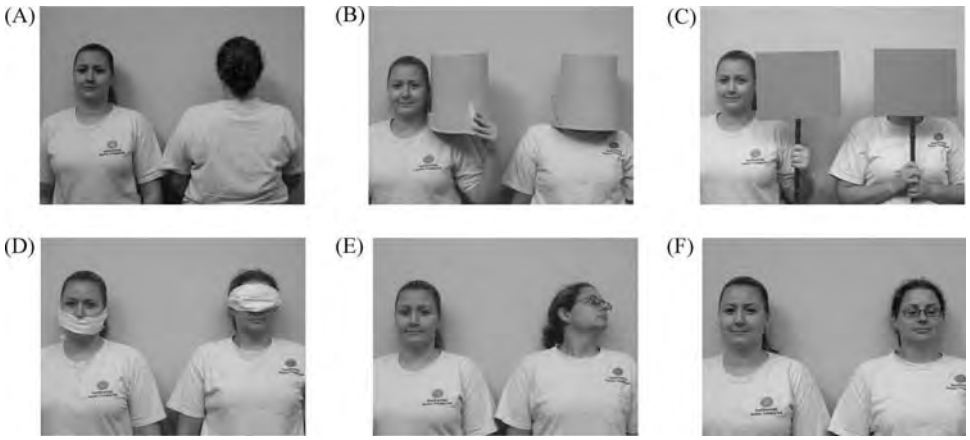


Figure 1. Experimental conditions presented in Experiment 1. (A) Front/back, (B) buckets, (C) screens, (D) blindfolds, (E) look at/look away, and (F) eyes open/eyes closed.

placed an identical bucket on her inside shoulder. In Condition 3, *screens*, both experimenters were oriented forward and one placed a cardboard screen (30.5 × 23 cm) in front of her face and the other placed it next to her face above her inside shoulder. In Condition 4, *blindfolds*, both experimenters were oriented forward and one placed a blindfold over her eyes and the other placed a blindfold over her mouth. In Condition 5, *look at/look away*, both experimenters were oriented forward and one looked straight ahead at the subject while the other looked up and away toward the outside. Finally, in Condition 6, *eyes open/eyes closed*, both experimenters were oriented forward and one experimenter looked straight ahead at the subject with her eyes open and the other looked straight ahead with her eyes closed. Conditions and sessions were counterbalanced for side (left/right) and experimenter (E1/E2). For all trials both experimenters stood 76.2 cm back from the cage mesh and approximately 90 cm apart holding a 3-ounce cup of sugar-free gelatin. Once the subject was sitting in front of and attending to the experimenters, the food items were presented in each experimenter's outside hand simultaneously and the subject had up to 1 min to make a choice. The seeing experimenter determined when a choice was made. If the subject chose correctly, they received the food reward. If they were incorrect, they received nothing, and experimenters proceeded to the next trial. The gorillas' responses were recorded at the end of each trial. In addition, all experimental trials were video-recorded for post hoc analysis. A second observer, naive to the experimental conditions, coded about 20% of Experiment 1 trials for reliability. Interrater reliability between coders showed 94.6% agreement (Cohen's Kappa, $\kappa = 0.89$).

Results and Discussion

For each of the six conditions, the mean percentage of correct responses was calculated in order to evaluate overall performance at the group level. A paired *t* test comparing group performance between Set A and Set B showed that there was no learning effect for any condition: front/back ($M_A = 85.67\%$, 95% CI_A [75.72, 95.62]; $M_B = 94.00\%$, 95% CI_B [87.10, 100.00]; $t(5) = 1.60$, $p = .1695$), buckets ($M_A = 52.33\%$, 95% CI_A [37.13, 67.54]; $M_B = 62.83\%$, 95% CI_B [40.76, 84.91]; $t(5) = 0.96$, $p = .3815$), screens ($M_A = 60.67\%$, 95% CI_A [45.10, 76.23]; $M_B = 60.67\%$, 95% CI_B [50.72, 70.62]; $t(5) = 0.00$, $p = 1.0000$), blindfolds ($M_A = 52.33\%$, 95% CI_A [32.99, 71.68]; $M_B = 48.17\%$, 95% CI_B [38.36, 57.98]; $t(5) = 0.47$, $p = .6607$), look at/look away ($M_A = 64.83\%$, 95% CI_A [49.36, 80.31]; $M_B = 64.83\%$, 95% CI_B [55.02, 74.64]; $t(5) = 0.00$, $p = 1.0000$), and eyes open/eyes closed ($M_A = 67.00\%$, 95% CI_A [60.50, 73.50]; $M_B = 60.67\%$, 95% CI_B = [50.72, 70.62]; $t(5) = 2.23$, $p = .0759$). Given these results, data from Set A and Set B were averaged in order to allow for direct comparison in later experiments. The gorillas' group performance against chance level (0.50) was assessed using one-sample *t* tests. This calculation showed that in Experiment 1 the gorillas performed significantly above chance on four conditions: front/back ($M = 89.83\%$, $t(5) = 18.65$, $p < .0001$), look at/look away ($M = 64.67\%$, $t(5) = 3.50$, $p = .0172$), eyes open/ eyes closed ($M = 63.67\%$, $t(5) = 4.51$, $p = .0063$), and screens ($M = 60.50\%$, $t(5) = 2.98$, $p = .0309$). Subjects performed at chance level on the bucket ($M = 57.50\%$, $t(5) = 1.52$, $p = .1898$) and blindfold ($M = 50.17\%$, $t(5) = 0.04$, $p = .9680$) conditions (see Figure 2).

An ANOVA on the percentage of correct choices with condition as a variable revealed that the gorillas did indeed treat conditions differently, $F(5, 25) = 14.04$, $p < .001$, $\omega^2 = 0.72$. However, a series of post hoc *t* tests showed a significant difference in performance only between the front/back and blindfold conditions, $t(5) = 6.073$, $p < .05$.

Individual data were also analyzed per subject to examine individual differences as well as to elucidate the possible response strategies employed by each gorilla. Based on Experiment 1 performance, three possible strategies were identified by the experimenters. The use of body orientation, the use of head orientation, and the use of naturally occurring, socially relevant cues were all evaluated for each subject. Fisher's exact tests show that all but one gorilla discriminated based on body orientation: front/back vs. all other conditions; Haloko ($p = .0059$), Kwame ($p = .0042$), Mandara ($p = .0175$), Baraka ($p = .0175$), and Kigali ($p = .0484$). However, only three subjects appeared to discriminate based on head orientation: front/back + look at/look away vs. all other conditions; Haloko ($p = .0320$), Mandara ($p = .0113$), and

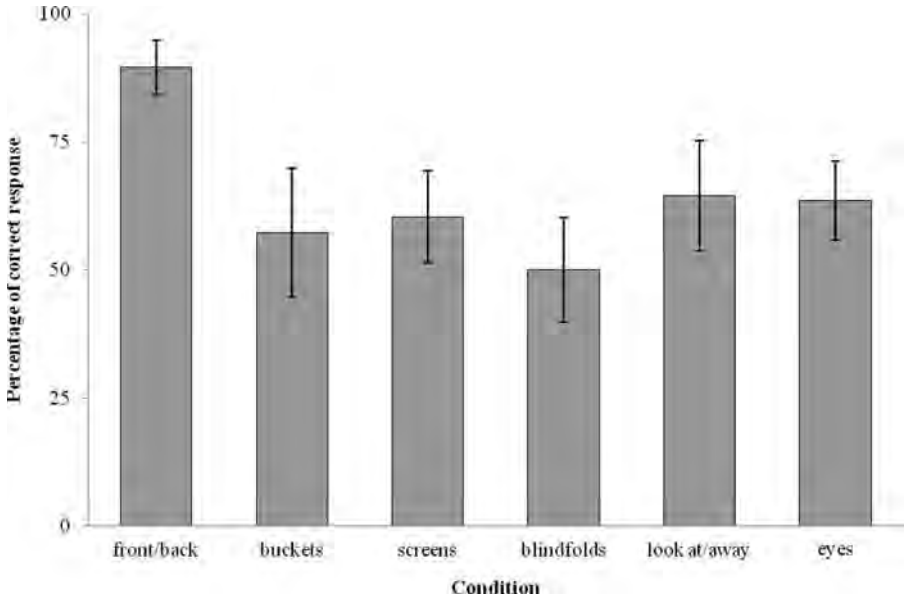


Figure 2. Gorillas' performance in Experiment 1 by condition as a percentage of correct responses. Error bars represent 95% confidence interval.

Baraka ($p = .0113$). Similarly, two of those same three subjects appeared to excel in any condition that was more naturally occurring, rather than employing the use of an object (front/back + look at/look away + eyes open/eyes closed vs. buckets head/bucket shoulder + screen front/ screen side + blindfold eyes/blindfold mouth: Baraka ($p = .0166$) and Mandara (approaching significance, $p = .0505$). One subject, Kojo, also seemed to follow this trend, but an outstanding performance in the first of two blindfold condition sessions affected statistical tests.

Overall, the gorillas' performance in Experiment 1 did not suggest that they were following either of the perceptually based rules (i.e., the "face rule" and "eye rule") proposed in previous studies (Povinelli & Eddy, 1996b; Reaux et al., 1999). Povinelli and Eddy (1996b) suggested that the bucket and screen conditions may be easier because although they require a subject to attend to the experimenter's head and face orientation, these conditions do not require more acute attention to the experimenter's eyes. However, the gorillas showed proficiency in discriminating whether an experimenter's eyes were available, but seemed to struggle with the conditions that involved the use of an object. It is possible that they were simply thrown by the unusual action of a human wearing a bucket or a blindfold, a normally uncommon occurrence. Alternatively, and more likely, it is possible that the conditions not employing the use of an object are more naturally occurring, thus allowing the gorillas more opportunity to learn the nuances of visual attention and their social relevance through daily social interactions. Presumably, this experience could drive their success in such object-free conditions. Given these results, it would seem that the gorillas were either not using perceptually based rules at all or were simply using different features to drive their judgments of attention.

Experiment 2

Procedure

Experiment 2 was designed to further investigate the various possible response strategies used by the gorillas in Experiment 1, particularly the gorillas' perception of body and head orientation. Experiment 2 used the same six subjects and the same experimenter protocols as in Experiment 1, but introduced three new conditions that were given over three sessions of eight trials each (see Figure 3). In Condition 1, *negative body orientation*, both experimenters stood with their backs to the subject. One experimenter remained oriented away and looking away from the subject, and the other looked over her shoulder, turning her head to



Figure 3. Experimental conditions presented in Experiment 2. (A) Negative body orientation, (B) neutral body orientation, and (C) contradictory body orientation.

face the subject. In Condition 2, *neutral body orientation*, the experimenters oriented toward each other so that each was perpendicular to the subject. One experimenter turned her head to face the subject, and the other turned her head away from the subject. In Condition 3, *contradictory body orientation*, one experimenter oriented away but looked over her shoulder toward the subject, and the other oriented toward but looked over her shoulder away from the subject. As in Experiment 1, all trials were video-recorded, and 20% were coded by a second naive observer. Interrater reliability between coders for Experiment 2 showed 100% agreement (Cohen's Kappa, $\kappa = 1$).

Results and Discussion

As in Experiment 1, a mean percentage of correct responses was calculated to evaluate performance at the group level and compared to chance (0.50) using one-sample *t* tests. This analysis shows that gorillas performed at chance level, $M = 54.33\%$, $t(5) = 0.83$, $p = .4463$, on the *negative* condition, where they were faced with two experimenters who were oriented backward. It seems that they were unable to overcome this strong negative body orientation cue and defaulted to a side bias, rather than choosing the experimenter whose face was turned and visible. Evaluating the *contradictory* condition adds strength to this hypothesis as the gorillas significantly chose the incorrect experimenter, $M = 25.33\%$, $t(5) = 2.69$, $p = .0434$; that is, the gorillas chose the person oriented toward them even though the person was looking away rather than the person oriented away whose head and eyes were turned toward them. Further, the gorillas' performance improved greatly in the *neutral* condition, which eliminated the presence of an overt body orientation. Their performance was significant on this final condition, $M = 89.83\%$, $t(5) = 10.44$, $p < .0001$ (see Figure 4). A repeated-measures ANOVA confirmed that the gorillas responded to each condition differently ($F_{2,10} = 51.705$, $p < .0001$, $\omega^2 = 0.75$). A series of post hoc *t* tests showed a significant difference in performance between the negative and neutral conditions, $t(5) = 5.660$, $p < .05$; negative and contradictory conditions, $t(5) = 4.624$, $p < .05$; and neutral and contradictory conditions, $t(5) = 10.205$, $p < .05$. Overall, results from Experiment 2 indicate that body orientation is the strongest and most salient indicator of visual attention for the gorillas. However, in the presence of a less overt body orientation, the gorillas seem to look to the face of the experimenter to gain more information.

Experiment 3

Procedure

Given the results of Experiment 2, Experiment 3 was designed to test the gorillas' performance on the original conditions using a neutral, side-facing body posture to see if this had an effect on their responses. Four familiar conditions: buckets, screens, blindfolds, and eyes open/eyes closed, were tested over four sessions of eight trials each. The conditions were similar to those in Experiment 1, except that both experimenters presented the conditions while facing to the side (toward each other) and turning their heads to look at the subject (see Figure 5). The same six subjects participated in this experiment, and general experimental protocols remained the same as in previous experiments. Also as in previous experiments, all trials were video-recorded, and 20% were coded by a second naive observer. Interrater reliability between coders for Experiment 3 showed 100% agreement (Cohen's Kappa, $\kappa = 1$).

Results and Discussion

Again, the mean percentage of correct responses was calculated for each condition in order to evaluate group level performance. This group mean was then compared to chance (0.50) using one-sample *t* tests. These tests show that the gorillas were significantly correct in the side-bucket, $M = 77.33\%$, $t(5) = 3.63$, $p = .0150$; side-screen, $M = 69.17\%$, $t(5) = 4.51$, $p = .0063$; and the side-eyes open/eyes closed, $M = 79.17\%$, $t(5) = 3.80$, $p = .0127$, conditions. Their performance on the side-blindfold condition was not significant, $M = 62.83\%$, $t(5) = 1.78$, $p = .1355$. Regardless, the subjects' group performance did improve in all conditions in Experiment 3 when compared to Experiment 1 (see Figure 6).

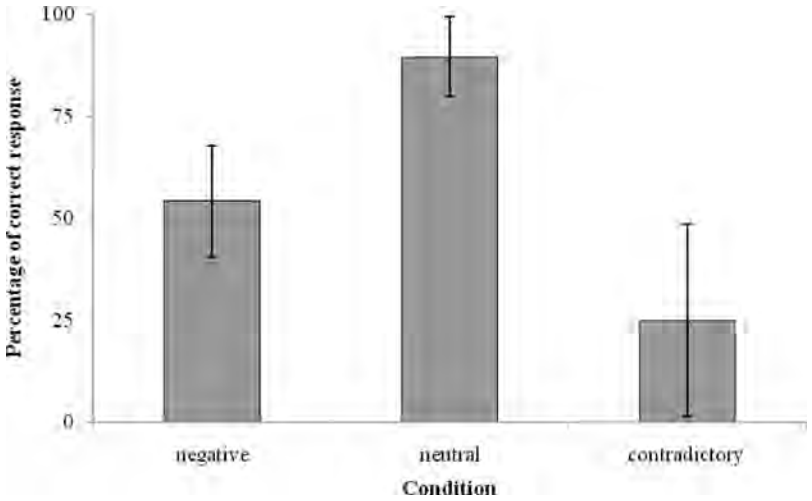


Figure 4. Gorillas' performance in Experiment 2 by condition as a percentage of correct responses. Error bars represent a 95% confidence interval.

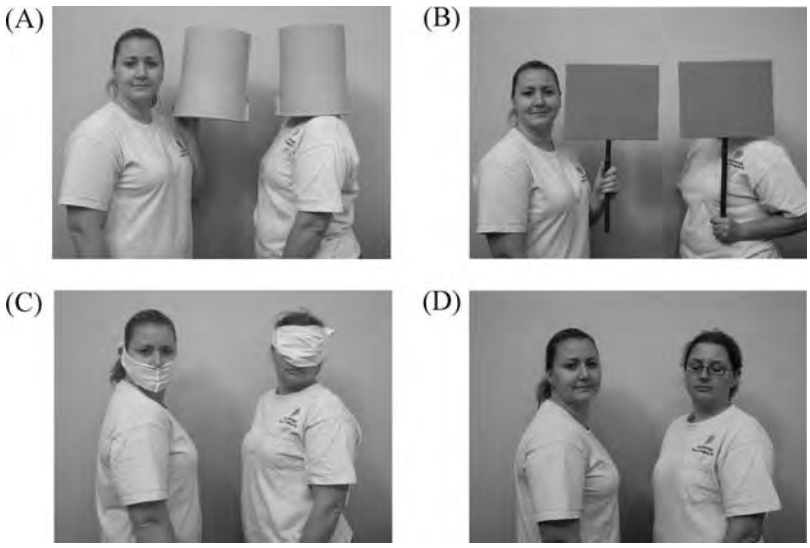


Figure 5. Experimental conditions presented in Experiment 3. (A) Side-buckets, (B) side-screens, (C) side-blindfolds, and (D) side-eyes open/eyes closed.

To further examine the gorillas' improved performance, paired *t* tests were conducted comparing the mean performance between Experiment 1 and Experiment 3 by condition. These calculations show a significant difference in both the screen: $M_1 = 60.50\%$, 95% CI_1 [51.43, 69.57]; $M_3 = 69.17\%$, 95% CI_3 [58.25, 80.08]; $t(5) = 2.75$, $p = .0402$, and the eyes open/eyes closed, $M_1 = 63.67\%$, 95% CI_1 [55.88, 71.45]; $M_3 = 79.17\%$, 95% CI_3 [59.42, 98.92], $t(5) = 2.95$, $p = .0320$, conditions. As a group, the gorillas did not show significant improvement in the bucket, $M_1 = 57.50\%$, 95% CI_1 [44.79, 70.21]; $M_3 = 77.33\%$, 95% CI_3 [57.99, 96.68]; $t(5) = 1.90$, $p = .1158$, or blindfold, $M_1 = 50.17\%$, 95% CI_1 [40.01, 60.33]; $M_3 = 62.83\%$, 95% CI_3 [44.28, 81.39]; $t(5) = 2.28$, $p = .0715$, conditions. One subadult male (Kwame), performed consistently below the group average across all experiments. In fact, he was the only subject whose performance was poorer on the bucket and blindfold conditions in Experiment 3 than in Experiment 1. When his Experiment 3 results are removed from the group analysis, the difference in bucket, $M_1 = 55.10\%$, 95% CI_1 = [44.60, 65.60]; $M_3 = 82.80\%$, 95% CI_3 = [70.38, 95.22]; $t(4) = 3.23$, $p = .0319$, and blindfold, $M_1 = 51.40\%$, 95% CI_1 = [43.50, 57.10]; $M_3 = 67.80\%$, 95% CI_3 = [55.23, 80.37]; $t(4) = 3.26$, $p = .0312$, conditions become significant as well. These results show that the neutral side-facing condition did seem to aid the gorillas in making better determinations of the experimenter's visual attention in some cases. We cannot rule out the possibility that the improved performance in Experiment 3 is due to learning

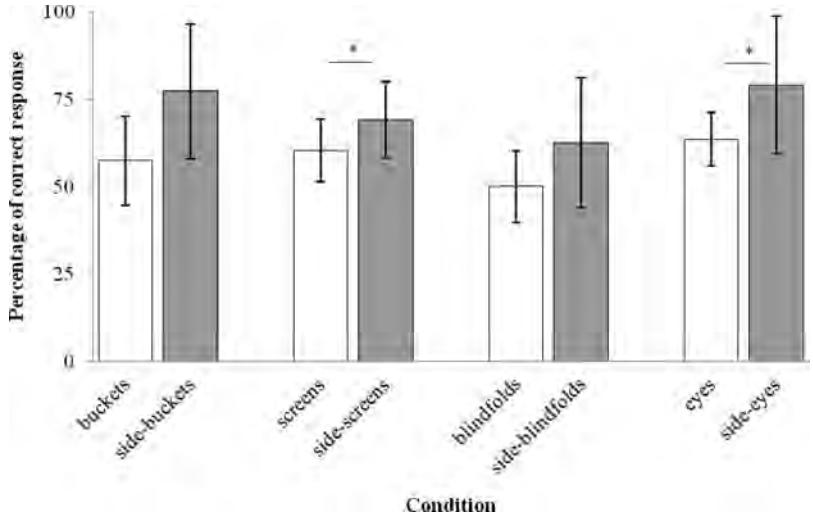


Figure 6. Comparison of gorillas' performance in Experiment 3 to performance in Experiment 1 by condition as a percentage of correct responses. Error bars represent a 95%. confidence interval, and asterisk (*) indicates significant difference in group performance between experiments, $p < .05$.

effect. However, the fact that performance did not change between Experiment 1 and Experiment 2, but greatly improved in Experiment 3 when body orientation was experimentally manipulated, offers strong support of alternative hypotheses.

General Discussion

There were two main findings from this study. First, we found that the gorillas were successful in choosing the appropriate human experimenter not only when body orientation could be used as an indicator, but also when they had to make a discrimination based on an experimenter's eyes: a condition where many other great apes have performed poorly (Kaminski et al., 2004; Povinelli & Eddy, 1996b; Reaux et al., 1999; Theall & Povinelli, 1999). The gorillas did not seem to make use of the perceptually based "face rule" or "eye rule" proposed by Povinelli and Eddy (1996b), but may have used other means to determine attention. One possibility is that the gorillas were not using perceptually based rules, but rather inherently understand the connection between one's eyes and their ability to see and perceive. However, such a strong conclusion is contradicted by the subjects' poor performance discriminating between the seeing and nonseeing experimenter in the bucket and blindfold conditions. A more likely explanation is that gorillas are employing different perceptually based rules that have been learned not over the course of an experimental session, but gradually over a lifetime in their daily interactions both with conspecifics and human caregivers. This can explain why the gorillas performed better on more naturally occurring conditions (i.e., front/ back, look at/look away, and eyes open/eyes closed), which were more relevant to their day-to-day lives and with which they would have had more experience. Povinelli and Eddy (1996b) proposed a similar hypothesis when evaluating the nearly perfect performance of their chimpanzees on the front/back condition versus their chance performance on the bucket and blindfold conditions. However, they quickly dismissed it after the chimpanzees performed again at chance levels on other more naturally occurring conditions.

Further, it has been suggested that enculturated apes may have the upper-hand in studies such as this one (Bulloch et al., 2008) because of their extensive experience with humans and human artifacts, enhancing their ability to make appropriate judgments of human attention as well as to generalize the physical properties of the objects used in some conditions. Although the National Zoo gorillas are not considered highly enculturated and are relatively inexperienced with working in a structured, experimental context, they performed particularly well in this study. For example, all six of the gorillas were correct on the first trial in the eyes open/eyes closed condition, lending strong support to the idea that the gorillas have at least a rudimentary understanding of the function of the eyes and the connection that they have to attention and are able to apply it to human experimenters.

The second major finding was that the gorillas appeared to be utilizing a hierarchical approach to making judgments of visual attention, attending to the most salient cue available first. Body orientation seemed to drive the gorillas' initial response in most cases, followed by head orientation and then features of the face. This phenomenon has been loosely suggested by researchers in studies of chimpanzees (Bulloch et al., 2008; Kaminski et al., 2004; Reaux et al., 1999), orangutans, and bonobos (Kaminski et al., 2004), who show similar response patterns. When faced with a pair of experimenters, one whose body was oriented forward toward the subject and the other whose body was oriented away, the gorillas selected the seeing experimenter with ease. When faced with a pair of experimenters who were both oriented away from the subjects, the gorillas chose at random regardless of the fact that one experimenter was looking over the shoulder at the subject. In this case, the negative body orientation seemed to provide a very strong message of "this person is not looking," which superseded any judgment of the face. Similarly, in the condition in which the body and face orientations of the experimenters were contradictory, the gorillas chose the person who was facing forward, even though the person was looking away, significantly more often than they chose the person who was oriented away, but looking back at them. Interestingly, apes in previous studies showed the same difficulty with this contradictory condition (Bulloch et al., 2008; Kaminski et al., 2004; Reaux et al., 1999). Kaminski et al. (2004) suggest that although face orientation is perceived as an indicator of attention, body orientation relates to an experimenter's inclination to transfer food. Experimental procedure in the current study was designed such that both experimenters presented a food reward in the same way, by extending the food out toward the subject, thus showing an ability to transfer the food. This methodological difference should have removed uncertainty in whether the gorillas were judging the attention or ability of experimenters.

When the gorillas were faced with two experimenters who were both oriented toward them, assessment of body orientation would not provide adequate information and would require them to then look to head orientation, which we propose is the second most salient cue. Indeed, the gorillas also performed well above chance in this situation. In the look at/look away condition, they were able to utilize head orientation as an indicator of attention. Lastly, when both the body and head orientation of both experimenters were forward-facing, the gorillas were required to make use of facial features to determine attention. In this situation, the gorillas' performance was variable. Although they performed significantly above chance in the eyes open/eyes closed and screens conditions, their performance on the buckets and blindfolds were only around chance level. Here, it is possible that the novelty of objects used in these conditions was distracting to the gorillas. It is also possible that their success on the eyes condition was an anomaly, although we feel that their success over several sessions rules this out.

Perrett and colleagues (Perrett & Emery, 1994; Perrett, Hietanen, Oram, & Benson, 1992) report a hierarchical organization in the sensitivity of cells in the temporal cortex of macaques responsive to heads and faces. They found that in these cells, sensitivity and response to head cues override body cues, and eye cues, in turn, override head cues. Perrett et al. (1992) suggested that the eyes provide the most salient cue of attention, and only when eye direction is not clear, would one consider head orientation. Similarly, they suggest that when the head cannot be seen, then information from body posture could be used to judge attention. Although we suggest that the gorillas are using these visual cues with the opposite priority, the underlying idea of a hierarchical structure is the same.

Ecologically, a quick "snapshot" overview of the attentional state of others would serve gorillas well in social situations where they regularly monitor the position of group members as well as in

high stress situations where quick judgments of those around them would be necessary. Here, the "snapshot" would reasonably make use of the most blatant attentional feature available, the body. In addition, when moving through a complex, dense environment, such as a forest, reliance on judging one's visual attention based on their eyes would prove to be ineffective at best.

From a behavioral perspective, the social structure of a gorilla troop is much more stable and relaxed than that of the chimpanzee. Although chimpanzees live in a fluid fission-fusion society in which group members are constantly moving into and out of subgroups, gorilla troops are stable for long periods of time, and they feed and travel as one group. Chimpanzees also have a more volatile and political hierarchy, whereas gorillas generally do not. Given their dynamic social structure and greater need to attend to the behavior of conspecifics, it would be more beneficial for chimpanzees to have developed a better appreciation of visual attention. Alternatively, gorillas may have less of a need for these skills because there is lower demand of their attention to other group members.

Evolutionarily, in contrast to the white sclera that humans possess, the pigmented sclera of great apes is a dark brown and provides little contrast to their iris and pupil, and in most cases the face as well. This physiological difference could drive the dependence on using other cues such as body and head orientation, because identifying the direction of gaze in a conspecific can be quite difficult. In fact, this appears to be an evolutionary adaptation that camouflages gaze, making it more difficult for conspecifics to detect direct eye contact, which can be perceived as a threat (Doherty, 2009). Also, it is not as common for primates other than humans to regularly move their eyes independently of their heads. Kobayashi and Kohshima (2001) found that although humans moved their eyes without a corresponding head turn roughly 60% of the time, chimpanzees only did so about 25% of the time. Smaller primates did this even less. Why then should nonhuman primates develop the ability to appreciate acute eye gaze in making judgments of attention when using head orientation proves very reliable? Eye movement that is independent of head movement, and the development of a contrasting white sclera are uniquely human adaptations. It stands to reason that the ability to appreciate these features may be uniquely human as well. In fact when gaze-following behavior in great apes and human infants was examined experimentally, Tomasello, Hare, Lehmann, and Call (2007) found that apes preferentially followed head direction, whereas infants followed eye direction.

For all of these reasons, we would expect the gorillas' performance on the eyes open/eyes closed condition to be poor, but in fact found just the opposite. Overall, the gorillas' performance across this study and how it relates to Theory of Mind can be interpreted in different ways. Understanding visual perception and attention is generally regarded a precursor to but not evidence of Theory of Mind. We suggest that the development of this hierarchical response strategy had to be based in some understanding of the mechanisms of visual attention, that is, that the eyes and their orientation are connected to one's ability to see and perceive things in the environment. What we propose is that the subjects' understanding of these mechanisms does not simply stem from a series of discretely learned associations as Povinelli and colleagues (Povinelli & Eddy, 1996b; Reaux et al., 1999) suggest, but rather a general understanding of visual attention developed early in life that can be flexibly applied.

References

Andrews, K. (2005). Chimpanzee theory of mind: Looking in all the wrong places? *Mind & Language, 20,* 521–536.

Babitz, M. A. (2000). [Gorilla tool use]. Unpublished raw data.

Bulloch, M. J., Boysen, S. T., & Furlong, E. E. (2008). Visual attention and its relation to knowledge states in chimpanzees, *Pan troglodytes. Animal Behaviour, 76,* 1147–1155.

Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Science, 12,* 187–192.

Doherty, M. J. (2009). *Theory of mind: How children understand others' thoughts and feelings.* New York, NY: Psychology Press.

Gomez, J. C. (1991). Visual behavior as a window for reading the mind of others in primates. In A. Whiten (Ed.), *Natural theories of mind* (pp. 195–207). Oxford, England: Blackwell.

Hostetter, A. B., Cantero, M., & Hopkins, W. D. (2001). Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology, 115,* 337–343.

Hostetter, A. B., Russel, J. L., Freeman, H., & Hopkins, W. D. (2007). Now you see me, now you don't: Evidence that chimpanzees understand the role of the eyes in attention. *Animal Cognition, 10,* 55–62.

Kaminski, J., Call, J., & Tomasello, M. (2004). Body orientation and face orientation: Two factors controlling apes' begging behaviors from humans. *Animal Cognition, 7,* 216–223.

King, C. (2012). Gorillas' use of the escape response in object choice memory tests. Manuscript submitted for publication.

Kobayashi, H., & Kohshima, S. (2001). Unique morphology of the human eye and its adaptive meaning: Comparative studies on external morphology of the primate eye. *Journal of Human Evolution, 40,* 419–453.

Leavens, D. A., Hostetter, A. B., Wesley, M. J., & Hopkins, W. D. (2004). Tactical use of unimodal and bimodal communication by chimpanzees, *Pan troglodytes. Animal Behaviour, 67,* 467–476.

Liebal, K., Pika, S., Call, J., & Tomasello, M. (2004). To move or not to move: How apes adjust to the attentional states of others. *Interaction Studies, 5,* 199–219.

Penn, D. C., & Povinelli, D. J. (2007). On the lack of evidence that non-human animals possess anything remotely resembling a "theory of mind." *Philosophical Transactions of the Royal Society B: Biological Sciences, 362,* 731–744.

Perrett, D. I., & Emery, N. J. (1994). Understanding the intentions of others from visual signals: Neurophysiological evidence. *Current Psychology of Cognition, 13,* 683–694.

Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society B: Biological Sciences, 335,* 23–30.

Poss, S. R., Kuhar, C., Stoinski, T. S., & Hopkins, W. D. (2006). Differential use of attentional and visual communicative signaling by orangutans (*Pongo pygmaeus*) and gorillas (*Gorilla gorilla*) in response to attentional status of a human. *American Journal of Primatology, 68,* 978–992.

Povinelli, D. J., & Eddy, T. J. (1996a). Factors influencing young chimpanzees' (*Pan troglodytes*) recognition of attention. *Journal of Comparative Psychology, 110,* 336–345.

Povinelli, D. J., & Eddy, T. J. (1996b). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development, 61,* 1–152.

Povinelli, D. J., & Vonk, J. (2003). Chimpanzee minds: Suspiciously human? *Trends in Cognitive Sciences, 7,* 157–160.

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences, 4,* 515–526.

Reaux, J. E., Theall, L. A., & Povinelli, D. J. (1999). A longitudinal investigation of chimpanzees' understanding of visual perception. *Child Development, 70,* 275–290.

Shillito, D. J., Gallup, G. G., & Beck, B. B. (1999). Factors affecting mirror behavior in western lowland gorillas (*Gorilla gorilla*). *Animal Behaviour, 57,* 999–1004.

Swartz, K. B., & Estocsin, C. (2006). [Gorilla memory]. Unpublished raw data.

Theall, L. A., & Povineli, D. J. (1999). Do chimpanzees tailor their gestural signals to fit the attentional states of others? *Animal Cognition, 2,* 207–214.

Tomasello, M., Call, J., & Hare, B. (2003). Chimpanzees versus humans: It's not that simple. *Trends in Cognitive Sciences, 7,* 239–240.

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,* 314–320.

Received July 9, 2011
Revision received October 27, 2011
Accepted October 31, 2011 ■