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Now you see me, now you don't: evidence that chimpanzees understand the role of the eyes in attention

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Abstract

Chimpanzees appear to understand something about the attentional states of others; in the present experiment, we investigated whether they understand that the attentional state of a human is based on eye gaze. In all, 116 adult chimpanzees were offered food by an experimenter who engaged in one of the four experimental manipulations: eyes closed, eyes open, hand over eyes, and hand over mouth. The communicative behavior of the chimpanzees was observed. More visible behaviors were produced when the experimenter's eyes were visible than when the experimenter's eyes were not visible. More vocalizations were produced when the experimenter's eyes were closed than when they were open, but there were no differences in other attention getting behaviors. There was no effect of age or rearing history. The results suggest that chimpanzees use the presence of the eyes as a cue that their visual gestures will be effective.

Keywords

Chimpanzees; Visual attention; Communication; Gesture; Eye gaze

Introduction

From early in life, humans understand that the direction of someone's eyes is an important indication of what is being attended to. By age one, infants will reliably follow the gaze of their mother (Butterworth and Jarrett 1991). By age two, children will not turn to look in the direction an adult's head has turned if the adult's eyes are closed or occluded (Brooks and Meltzoff 2003). This understanding that another's eyes signal what he or she is attending to is particularly important for the development of communication. For example, children as young as 1 year of age begin to use pointing gestures to direct the gaze of adults, and carefully monitor the gaze direction of an adult (Franco and Butterworth 1996). By 18 months, children are able to successfully pair a verbally uttered label with the object that the adult was visually attending to at the time of labeling (Baldwin and Moses 1994). For humans, the ability to follow another's gaze and determine what he or she can and cannot see is an important part of developing successful communication skills.

As a building block to communication, the ability to reliably detect what others are attending to would seem to be useful for any social species, not just humans. Indeed, humans are not alone in their ability to follow others' eye gaze; rather, it is a skill shared by other species including dogs (Hare and Tomasello 1999, but see Agnetta et al. 2000) and primates (Brauer et al. 2005; Povinelli and Eddy 1996a; Tomasello et al. 1998). However, despite the evidence that other species can follow eye gaze, there is much debate about what, if any, cognitive understanding these other species have about the importance of eye gaze in attention. The tendency to follow the eye gaze of another individual may be instinctual, with other species having virtually no understanding of what eye gaze signifies. Alternatively, some species may learn to follow eye gaze over the course of development as they learn that doing so can lead to interesting discoveries. Again, this type of learning would not require any real cognitive understanding of eye gaze as a signal of attention in another individual. Finally, it is also possible that some species, like humans, come to understand that the direction of another's eyes determines what he or she does and does not see. This knowledge of "seeing" would then allow the species to understand another's current mental state and to predict the other's future behavior based on this mental state.

Much of the debate over gaze following comes from disagreement about whether other species are capable of understanding mental states at all, with the largest focus being on primates (Cheney and Seyfarth 1990; Heyes 1998; Povinelli 2003). In studies intended to determine what chimpanzees understand about the attentional states of others, investigators have typically compared the gestural and vocal behavior produced by a focal subject when an experimenter or conspecific is attending to the chimpanzee (e.g., facing the animal, making eye contact, and/or engaging in species typical head movements) to the behavior produced when the experimenter or conspecific is not attending to the chimpanzee. Several studies have found evidence that chimpanzees differentiate between an attentive audience and an inattentive audience, such that they direct more visual gestures (e.g., species typical begging gestures made with the hand extended outward and palm oriented up) toward an individual who is oriented toward them than toward an experimenter who is oriented away from them (Hostetter et al. 2001; Kaminski et al. 2004; Krause and Fouts 1997; Leavens et al. 2004; Liebal et al. 2004; Tomasello et al. 1994).

It has been argued, however, that when chimpanzees distinguish between an "attentive" and an "inattentive" individual, they are not necessarily making a mental attribution. Rather, it is possible that they have learned through experience that rewards are more likely when their audience is oriented toward them (Povinelli 2003; Heyes 1998). Povinelli (2003) found, for example, that the chimpanzees in his studies quickly learned to gesture in front of a forward-facing experimenter rather than a backward-facing experimenter. The chimpanzees were unable, however, to spontaneously transfer this knowledge to a condition where both experimenters faced forward, but one had her eyes open and the other had her eyes closed. Povinelli concluded that what the chimpanzees were doing in the backward/forward manipulation was relying on a "low-level" set of rules (*gesture to the experimenter whose face is visible*) rather than a "high-level" understanding of mental states (*gesture to the experimenter who can see me*).

Such an explanation is unlikely, however, if chimpanzees also react to individuals who are oriented away from them, but differentiate their behavior to produce more auditory or tactile based gestures when the other cannot see them. Indeed, Hostetter et al. (2001) and Leavens et al. (2004) found evidence that chimpanzees are faster to produce vocalizations and other auditory or tactile based gestures when an experimenter is inattentive than when the experimenter is attentive. This evidence suggests that chimpanzees do not simply believe that any behavior is more likely to be rewarded when an audience is oriented toward them, but rather, understand that it is specifically visual gestures that are more likely to be rewarded in these circumstances. Auditory or tactile gestures, on the other hand, can be used to get an inattentive individual's attention so that a visual gesture will be more effective.

Not all studies have found evidence supporting the hypothesis that chimpanzees understand the role that auditory and tactile gestures can have in gaining another's attention. Theall and Povinelli (1999) did not find an increase in chimpanzees' attention getting auditory or tactile gestures when a human experimenter was not attending over a situation where the experimenter was attending. Liebal et al. (2004) observed chimpanzees interacting with other chimpanzees. They also found no evidence that auditory or tactile based gestures were used more frequently when a recipient was not attending than when the recipient was attending (but see Tomasello et al. 1994).

There are several possible reasons for this discrepancy in experimental findings. Liebal et al. (2004) observed mainly situations where the recipient of an interactive gesture was attentive; they may not have had enough data regarding communication with an inattentive recipient to demonstrate a reliable pattern. Furthermore, the chimpanzees observed by Liebal et al. were free to move into each other's field of vision before initiating a gesture, thereby making the use of auditory or tactile gestures as attention getters unnecessary. It seems that, when given an opportunity to use a visual rather than a tactile or auditory cue, chimpanzees will reposition themselves so they can use a visible signal. Theall and Povinelli (1999) observed a very small number of young chimpanzees, raising the possibility that their failure to find evidence for differential use of auditory and tactile gestures could have been due to low statistical power or an as-yet undeveloped understanding of attentional states. Furthermore, Theall and Povinelli manipulated attentional state through eye gaze. The experimenters were always oriented toward the chimpanzee but were either looking at the chimpanzee with eyes open, looking at the chimpanzee and making head movements designed to resemble movements made by chimpanzees, "looking" at the chimpanzee with eyes closed, or gazing above the chimpanzee's head. It is thus possible that the cues chimpanzees use to differentiate between an attentive and inattentive audience are more global signs of body posture or orientation (as was manipulated in Hostetter et al. 2001; Leavens et al. 2004), rather than eye gaze per se.

In fact, Kaminski et al. (2004) found no evidence that apes produced communicative behaviors on the basis of eye gaze alone. Apes did not produce more behaviors toward an experimenter whose eyes were open than toward an experimenter whose eyes were closed. However, the same apes did alter their behavior on the basis of the experimenter's body orientation and (in some cases) face orientation. Unfortunately, Kaminski et al. did not analyze visual gestures separately from auditory and tactile gestures. Even though the apes did not produce fewer behaviors overall when the experimenter's eyes were closed, it is possible that they produced fewer visual gestures compared to when the experimenter's eyes were open. This decrease in visual gestures may have been accompanied by an increase in auditory or tactile gestures, making the total number of behaviors produced look very similar across conditions.

In the present study, we tested whether or not chimpanzees differentiate their communicative behavior based on the eye gaze of an experimenter. Specifically, we tested whether chimpanzees produce more visual gestures when an experimenter's eyes are visible and more auditory or tactile gestures when an experimenter's eyes are not visible. We used a paradigm that is similar to paradigms that have previously yielded support for chimpanzee understanding of attention (Hostetter et al. 2001; Kaminski et al. 2004; Leavens et al. 2004), but manipulated eye gaze rather than body orientation. A large number of adult chimpanzees were observed as they reacted to a situation within the context of their captive routine. The chimpanzees are often offered food in their social groups (which range from 2 to 18 animals), a situation that draws multiple animals from the social group toward the front of their enclosure, where they attempt to receive the food offer from the experimenter or care giver. In their attempts to receive the food, the chimpanzees engage in many behaviors including manual and facial gestures, vocalizations, and attention getting behaviors (such as banging on the cage and spitting on or throwing objects toward the individual offering food). In the present study, we manipulated whether or not the experimenter could see the behavior of the chimpanzees by changing only the state of her eyes. In one manipulation, the experimenter's eyes were either open or closed. In a second manipulation, the experimenter's hand either covered her mouth or covered her eyes. These two manipulations were not unlike those used by Povinelli and colleagues. However, rather than offering a choice to the subjects, we instead evaluated the frequency of different communicative behaviors in each situation.

We hypothesize that if chimpanzees understand the eyes as the locus of attention and understand attention as a prerequisite for successful communication, then chimpanzees will be more likely to produce visual gestures when the experimenter's eyes are visible than when the experimenter's eyes are not visible. Furthermore, if this tendency is the result of learning over development that behavior is more likely to be rewarded when another's eyes are visible rather than not visible, then the chimpanzees should produce more of every type of behavior when the experimenter's eyes are visible rather than not visible. If, however, chimpanzees understand that the eyes signal an attentional state that is specific to their visual behaviors, then the production of auditory and tactile gestures (vocalizations and attention getting behaviors) should not show this same pattern. Moreover, if chimpanzees understand that their auditory and tactile gestures can be effective ways of gaining an inattentive audience's attention, then they should produce more of these gestures when the experimenter's eyes are not visible compared to when they are visible.

Method

Subjects

The sample included 116 chimpanzees (47 males, 69 females) ranging in age from 6 to 50 years old (M_{age} = 22.04, SD = 10.40). Fifty-eight of the chimpanzees were mother-reared and 58 were nursery-reared. All chimpanzees were housed at the Yerkes National Primate Research Center (YNPRC), Atlanta, Georgia, USA, which is fully accredited by the American Association for Laboratory Animal Care. They were fed a regular diet throughout the duration of this experiment, which includes vegetables, fruit, and primate chow.

Chimpanzees were tested in their normal enclosures in the company of other members from their social groups. Social groups range from 2 to 18 animals, and larger groups were separated so that there were no more than three other animals enclosed with a focal animal during testing. The enclosures vary in size depending on the size of social group, but all are at least 33 m^3 with an indoor and outdoor area. Wire mesh separated the experimenters from the chimpanzees at all times.

Procedure

Two experimenters were involved for the testing of each chimpanzee; E1 offered food to the focal animal while E2 stood off to the side and recorded the focal animal's behavior. To offer food, E1 first got the focal subject's attention by calling his name and assuring that he was positioned at the front of the cage. E1 then knelt down approximately 1 m in front of the subject's cage and held a banana in front of her while engaging in one of the four experimental manipulations. In the eyes-open condition, she kept her eyes open throughout the trial and looked directly at the focal chimpanzee. In the eyes-closed condition, she kept her eyes closed and remained oriented toward the front throughout the trial. In the mouth-covered condition, she placed one hand over her mouth with her fingers pressed tightly together so that the lower half of her face was not visible. As in the eyes-open condition, she looked directly at the focal chimpanzee throughout the trial. In the eyes-covered condition, she placed one hand over her eyes so that the upper half of her face was not visible and maintained a forward orientation. In all conditions, the experimenters wore protective gear, including a clear plastic face shield and surgical mask, which the chimpanzees are accustomed to seeing. In both the eyes-covered and mouth-covered manipulations, E1 placed her hand on the outside of her plastic face shield.

Once E1 was in position, E2 started a stopwatch to time a 60 s trial duration. During the trial, E2 recorded all behaviors produced by the focal chimpanzee and classified them according to a behavioral ethogram.[1] Any extension of one or both hands through the wire mesh of the cage in an apparent attempt to point to or beg for the food was classified as a *manual gesture* (see Goodall 1986;Leavens and Hopkins 1998). A facial expression produced by protruding the lips in a species-typical way was classified as a *lip pout*. Noises produced by the subject's mouth or throat were classified as *vocalizations*. Slapping the hands together in a quick and forceful way so as to create a loud noise was classified as a *clap*. Making noise by striking any part of the cage with hands or feet was classified as a *cage bang*. Expelling water or saliva from the mouth in the direction of the experimenter was classified as *spit*. Projecting chow or feces toward the experimenter from inside the cage was classified as *throw*. Attempts to push out objects from inside the cage in exchange for food was classified as *share*. Making the swelling or rump visible to the experimenter by pressing it against the cage mesh was classified as *present*. An aggressive display was classified as *display*. A subject's departure from the testing area or retreat to the back of the cage was classified as *leave*. Finally, any behavior that did not fall into one of these categories was classified as *other*.

Following each 60 s trial, E1 gave the banana to the focal subject, regardless of the behavior displayed during the trial. Chimpanzees received each of the four experimental manipulations only once in a counterbalanced order. No more than two trials were ever administered to the same focal animal on the same day, and trials were usually separated by several days. Subjects were randomly selected as focal subjects, with the stipulation that subjects in the same social group could not be tested after one another so that back-to-back trials were not administered at the same cage. The same experimenter served as E1 for all four manipulations for a given subject. Testing took place over the course of 30 months and was interspersed with testing on a variety of other behavioral tasks.

Reliability

To establish inter-rater reliability, the responses of ten chimpanzees to the four experimental conditions were videotaped. Data from one subject in one condition had to be discarded due to technological problems. Two independent observers who were blind to the experimental condition coded the behaviors of each subject in each condition. Agreement was high between the two coders for the total number of behaviors observed in each condition, $r(37)=0.92$, $p<0.001$. The two coders also agreed strongly about the number of gestures, $r(37)=0.92$, $p<0.001$, the number of vocalizations, $r(37)=0.91$, $p<0.001$, the number of other visual gestures (share, present, and lip pout), $r(37)=0.89$, $p<0.001$, and the number of attention getting behaviors (clap, cage bang, spit, and throw), $r(37)=0.98$,$p<0.001$, that were observed in each condition.

[1]The focal chimpanzee did not typically direct any communicative behaviors toward E2, because E1 clearly had the food. On the rare occasion that a communicative behavior was directed toward E2, it was not recorded.

Results

The primary question of interest in the present experiment was whether or not chimpanzees would alter their gestural, vocal, and attention getting behavior in accordance with whether or not an experimenter's eyes were visible. The visibility of the experimenter's eyes was manipulated in two different ways. In the first manipulation, the experimenter simply closed her eyes or left them open. In the second manipulation, she either covered her eyes with her hand or covered her mouth with her hand. Although both of these manipulations have the effect of making the experimenter's eyes invisible in one condition, it is not clear that the two manipulations are completely comparable. More specifically, the use of the experimenter's hand in the eyes-covered vs. mouth-covered manipulation might signal something about the experimenter's readiness to dispense food (i.e., the additional behavior makes her seem more preoccupied), in addition to her ability to see. We therefore analyzed the two manipulations separately.

Four dependent variables were created from the behavioral ethogram described above. *Manual gestures* and *vocalizations* were analyzed as separate variables. Because of their low frequency, lip pout, present, and share were collapsed into a category called *other visual gestures*. Similarly, clap, cage bang, spit, and throw were collapsed into a category of *attention getting behaviors*. These four dependent variables were analyzed with two separate MANOVAs; one comparing the behaviors produced in the eyes-open vs. eyes-closed manipulation, and one comparing the behaviors produced in the covered mouth vs. covered eyes manipulation. Follow up tests were performed using paired samples *t*-tests.

Eyes-open vs. eyes-closed

A 2 (condition: eyes-open, eyes-closed) × 4 (communicative behavior: manual gestures, other visual gestures, vocalizations, attention getting behaviors) MANOVA revealed a significant two-way interaction between test condition and behavior $F(3,113)=5.78$, $p=0.001$. The mean number of manual gestures, other visual gestures, vocalizations and attention getting behaviors observed in this test condition are shown in Fig. 1. The chimpanzees produced more manual gestures when the experimenter's eyes were open ($M=4.07$, SE=0.31) than when the experimenter's eyes were closed ($M=2.91$, SE=0.27), $t(115)=4.87$, $p<0.001$. Similarly, the chimpanzees produced more other visual gestures when the experimenter's eyes were open ($M=1.11$, SE=0.16) than when the experimenter's eyes were closed ($M=0.68$, SE=0.14), $t(115)=3.65$, $p<0.001$. In contrast, the chimpanzees vocalized more when the experimenter's eyes were closed ($M=4.11$, SE=0.85) than when the experimenter's eyes were open ($M=2.61$, SE=0.54), $t(115)=2.13$, $p=0.035$. No significant difference was found for the attention getting behaviors, $t(115)=0.46$, $p=0.65$. Chimpanzees produced just as many attention getting behaviors when the experimenter's eyes were open ($M=2.51$, SE=0.59) as they did when the experimenter's eyes were closed ($M=2.78$, SE=0.65).

Eyes-covered vs. mouth-covered

A second 2 (condition: eyes-covered, mouth-covered) × 4 (behavior: gestures, other visual gestures, vocalizations, attention getting behaviors) MANOVA was performed. Again, an interaction between condition and type of behavior emerged, $F(3,113)=4.01$, $p=0.009$. Figure 2 displays the mean number of each type of communicative behavior produced in these conditions. As in the eyes-open vs. eyes-closed manipulation, chimpanzees produced more gestures when the experimenters hand covered her mouth ($M=4.02$, SE=0.33) than when her hand covered her eyes ($M=2.83$, SE=0.26), $t(115)=4.78$, $p<0.001$. The chimpanzees also produced more other visual gestures when the experimenters eyes were not covered ($M=1.03$, SE=0.17) than when they were covered ($M=0.72$, SE=0.14), $t(115)=2.34$, $p=0.02$. Unlike the eyes-open vs. eyes-closed manipulation, there was no difference in the number of vocalizations produced when the experimenter's eyes were covered (*M*=3.53, SE=0.84) compared to when they were not covered (*M*=3.79, SD=0.81), $t(115)=0.61$, $p=0.54$. There was also no difference in the number of other attention getting behaviors, $t(115)=0.17$, $p=0.86$. Just as in the eyes-open vs. eyes-closed manipulation, chimpanzees produced the same number of attention getting behaviors when the experimenter's eyes were covered (*M*=2.58, SE=0.63) as they did when the experimenter's mouth was covered (*M*=2.65, SE=0.75).

Rearing history

If the ability to distinguish between an attentive and an inattentive experimenter is the result of learning, then chimpanzees that were reared by humans (and thus have more experience with humans) should show stronger effects than chimpanzees that were reared by their mothers (whether in the wild or in captivity). To test this possibility, difference scores were calculated comparing each individual's frequencies of behaviors in the eyes-closed condition with his frequencies of behaviors in the eyes-open condition. The same comparisons were also made with regard to the eyes-covered vs. mouth-covered conditions. These difference scores were then analyzed using independent samples *t*-tests to compare mother-reared animals with human-reared animals. Bonferroni's correction procedure was used to control the alpha level across multiple comparisons. No pairwise comparison was significant at this level ($p<0.006$) Table 1.

Age

If chimpanzees learn over the course of their captive experience that humans are more likely to respond to visual gestures when their eyes are visible, then it might be expected that older animals (who have been in captivity longer) would show a stronger effect than younger animals. To test this possibility, we correlated age with each of the difference scores described above. Only one correlation was significant; there is a negative relationship between age and the tendency to produce more attention getting behaviors when the experimenter's hand covered her mouth than when her hand covered her eyes, $r(114)= -0.28$, $p=0.003$. This is actually the opposite of what a learning account would predict; older animals are less likely than younger animals to use more attention getting behaviors when their audience's hand occludes her eyes. This, combined with the fact that there was no significant difference for attention getting behaviors produced in the eyes-covered vs. mouth-covered conditions by the overall sample, suggests that this correlation is a Type I error (Table 2).

Discussion

The results of the present experiment suggest that chimpanzees do recognize the eyes as an important indicator of whether or not a human experimenter will respond to their behavior. Specifically, when an experimenter's eyes were not visible, chimpanzees produced significantly fewer visual gestures (both manual gestures and other visible behaviors such as lip pouting, presenting, or sharing) than when the experimenter's eyes were visible. Importantly, the chimpanzees did not simply decrease all types of communicative behavior when the experimenter's eyes were not visible; rather, they differentially reduced their visual behaviors only. This was true both when the experimenter's eyes were closed as well as when they were covered with the experimenter's hand. This finding coincides with previous findings (Hostetter et al. 2001; Leavens et al. 2004; Liebal et al. 2004) and suggests that (a) chimpanzees produce visual gestures predominantly when their audience is able to see the gestures, and (b) chimpanzees can determine when their gestures will be successful based not just on body or head orientation, but also on the presence or absence of the eyes.

This finding cannot rule out the possibility that the chimpanzees have simply learned that visible gestures are more likely to be rewarded when their audience's eyes are visible than when their eyes are not visible. However, while they may have learned this from their interactions with other chimpanzees, it is doubtful that they learned it from their captive experiences with humans. First, the chimpanzees were only exposed to one trial of each experimental condition and were always rewarded regardless of their behavior. It is thus impossible for them to have learned the necessary stipulation within the context of this experiment. While some might argue that they could have learned the stipulation in other experiences with human caretakers, it would certainly be an unusual occurrence for these chimpanzees to interact with a human who is oriented toward them without her eyes open. If learning is involved, it seems much more likely that the chimpanzees would have learned the more obvious stipulation of a forward body orientation rather than the more subtle requirement of open and un-occluded eyes, especially since the two almost always co-occur in the chimpanzees' everyday experiences with human caretakers.

Additionally, if all or most of these results can be explained by learning over extended captive experiences, then one might predict associations between an individual chimpanzee's experience with humans and his communicative performance in the experimental contexts used in this study. We estimated each chimpanzee's experience with humans in two ways: rearing history and age. Subjects who were reared in a nursery by humans have had extensive contact with humans since they were very young, and thus have had more time to learn about effective ways to interact with them. In contrast, subjects who were reared by their mothers (either in captivity or in the wild) have had less experience interacting with humans and less of a need to learn how to interact with them effectively. Rearing history had no influence on the effects found in this study. Mother-reared animals differentiated their behavior just as much as human-reared animals. We also considered age as an estimate of each chimpanzee's experience with humans. Older subjects, because they have been in captivity longer, have had more time to learn the contingencies demanded by the manipulations of this experiment. However, there were no significant correlations supporting this conclusion. Apparently, the ability to attend to a human experimenter's eyes and communicate accordingly is not something that requires early and prolonged interaction with humans.

In short, the present experiment has provided evidence that chimpanzees can differentiate their behavior in accordance with the presence or absence of an experimenter's eyes. Specifically, they appear to understand that another's inability to see is exclusively relevant to the effectiveness of their visual behaviors and not to their auditory or tactile behaviors, as they do not produce vocalizations or other attention getting behaviors less when the experimenter's eyes are closed. In fact, in the eyes-open vs. eyes-closed manipulation, the chimpanzees vocalized *more* when the experimenter's eyes were closed than when they were open. This coincides with previous findings (Hostetter et al. 2001; Leavens et al. 2004) and suggests that chimpanzees may have some understanding that vocalizations can be an effective method of gaining someone's attention. However, the fact that the chimpanzees did not show the same pattern in the eyes-covered vs. mouth-covered manipulation suggests that this understanding is not as strong as their understanding regarding visible gestures.

These findings are in direct contrast to previous studies that also manipulated eye gaze and found no evidence for differential behavior (Theall and Povinelli 1999). Methodological differences between the two studies may be able to explain this discrepancy. Conclusions that chimpanzees are unable to understand mental or attentional states (Povinelli and Eddy 1996b; Reaux et al. 1999; Theall and Povinelli 1999) are based on experiments that rely heavily on a "triangulation" approach (see Heyes 1998). Triangulation requires first training the subjects to do something under a certain set of conditions (e.g., gesture to an experimenter who is facing forward rather than facing backward). Then, once the subjects have learned to perform successfully, a key aspect of the original set of conditions is changed (e.g., now both experimenters are facing forward, but only one has her eyes open). The crucial test in such paradigms is how successfully the subjects will perform on the first few transfer trials (before they have a chance to learn the new stipulations).

The problem with such a method is that it is unclear whether the chimpanzees consider the trained gestural behavior to be the same as their own natural gestural behavior, and it may be more appropriate to consider it as a learned response (much like pushing a lever) than as a communicative attempt. In fact, it could be argued that the pretraining used in these paradigms removes whatever communicative function manual gestures have for the apes and instead creates instrumental responses without communicative relevance. If the animals do not see the “gestural” response as communicative, then from their perspective, the task goal of sticking their hand out in front of the person who can see them is not immediately apparent. If the subjects do not immediately recognize what they are being asked to do (e.g., *choose the person who can see me* rather than *choose my favorite person or choose the person on the left*), then as the animals build experience with the task, they may form a rule-based strategy that is effective at getting the reward but that is not representative of the “highest level” of thinking the animals are capable of. When the situation is changed, so that the rule-based system will no longer differentiate the right response from the wrong response, the animals have no choice but to guess at either the answer or at the new rule. Their failure to guess correctly does not suggest that they have no true understanding of seeing, only that they had no understanding of the original trained task’s purpose.

It is therefore important to investigate what chimpanzees know about attentional and mental states using procedures that are more representative of the chimpanzees’ ecological experiences (see Hare 2001). The present experiment and others like it (Hostetter et al. 2001; Leavens et al. 2004) use a paradigm that is more typical of captive chimpanzees’ everyday experience (although interacting with a human who waits 60 s before responding is certainly not without its oddities). While such paradigms are less able to rule out alternative explanations, they are advantageous because they do not require the animals to do or understand anything other than what they already do in their everyday lives. When such paradigms are used, it appears that chimpanzees do understand the difference between someone who can see them and someone who cannot.

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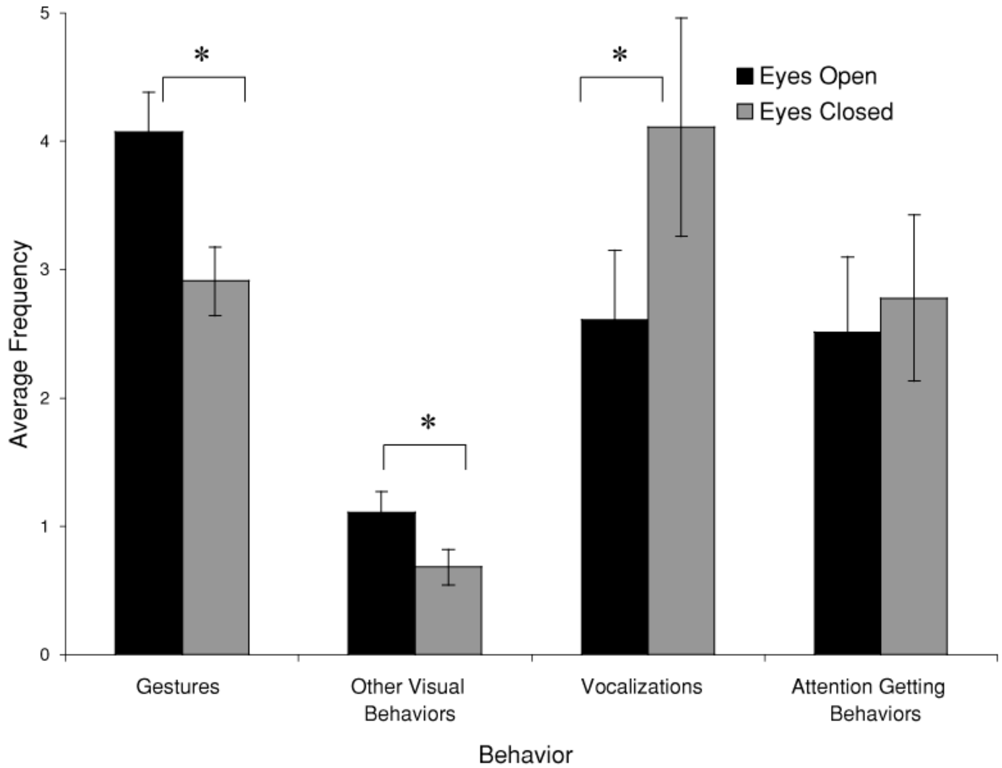

Fig. 1.
The mean number of communicative behaviors produced by the chimpanzees in the eyes-open and eyes-closed conditions. Error bars represent standard errors of the mean. (*) indicates a significant comparison, $p<0.05$

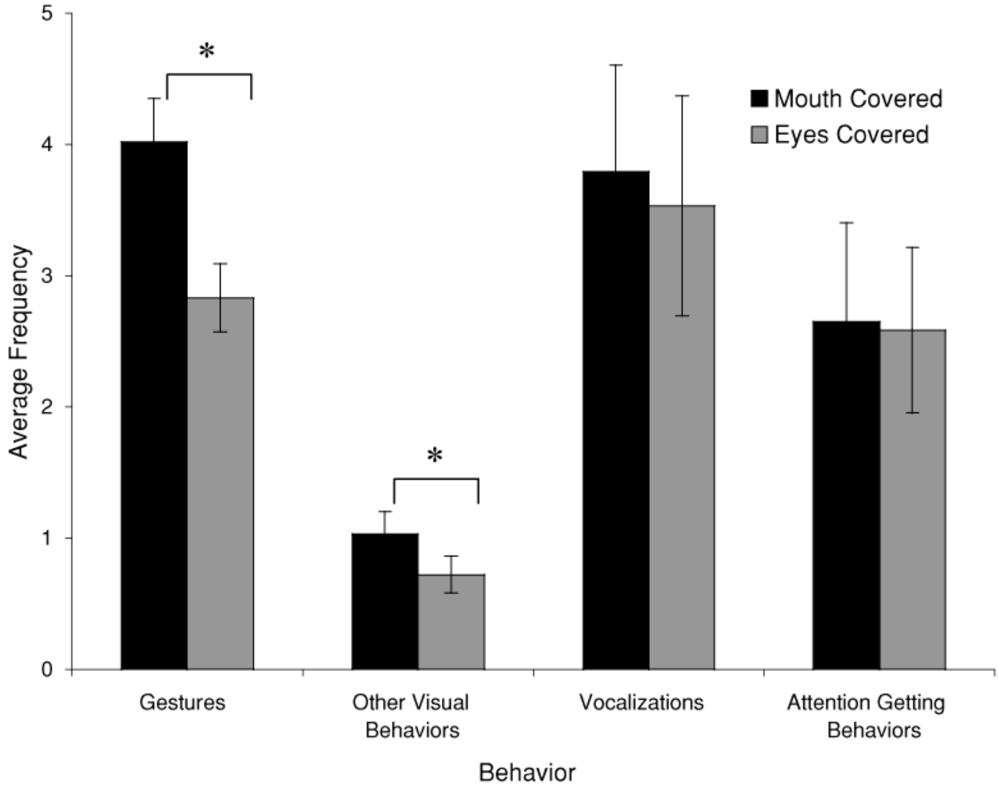

Fig. 2.

The mean number of communicative behaviors produced by the chimpanzees in the eyes-covered and mouth-covered conditions. Error bars represent standard errors of the mean. (*) indicates a significant comparison, $p<0.05$

Table 1

Average difference in frequency of behaviors produced in each experimental condition

	Mother-reared	**Human-reared**	***t*-value**	***p***
Eyes-closed vs. eyes-open				
Manual gestures	−0.76	−1.57	−1.71	0.09
Other visible gestures	−0.43	−0.43	0.00	1.00
Vocalizations	1.62	1.38	−0.17	0.87
Attention getting behaviors	0.40	0.14	−0.22	0.83
Eyes-covered vs. mouth-covered				
Manual gestures	−0.86	−1.52	−1.32	0.19
Other visible gestures	−0.22	−0.40	−0.65	0.52
Vocalizations	−1.31	0.78	2.43	0.02
Attention getting behaviors	−2.24	0.19	1.04	0.30

Negative values represent more behaviors being produced in the eyes visible condition than in the eyes invisible condition. A significant comparison is $p<0.006$, following Bonferroni adjustment for multiple comparisons

Table 2

Correlations between age and the difference in frequency of behavior between eyes invisible and eyes visible condition in each manipulation

	Eyes-closed vs. eyes-open		Eyes-covered vs. mouth-covered	
	r	***p***	***r***	***p***
Gestures	−0.06	0.55	0.07	0.44
Other visual gestures	−0.12	0.19	−0.03	0.72
Vocalizations	0.04	0.69	−0.04	0.68
Attention getting behaviors	0.08	0.42	−0.28	0.003

Negative values represent a tendency for older animals to demonstrate more behaviors when the experimenter's eyes were visible. A significant comparison is $p<0.006$, following Bonferroni adjustment for multiple comparisons