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Chimpanzees gesture to humans in mirrors: using reflection to dissociate seeing from line of gaze

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Abstract

There is much experimental evidence suggesting that chimpanzees understand that others see. However, previous research has never experimentally ruled out the alternative explanation that chimpanzees are just responding to the geometric cue of ‘direct line of gaze’, the observable correlate of seeing in others. Here, we sought to resolve this ambiguity by dissociating seeing from direct line of gaze using a mirror. We investigated the frequency of chimpanzees’ visual gestures towards a human experimenter who could see them (as a result of looking into a mirror) but who lacked a direct line of gaze to them (as a result of having his/her head turned away). Chimpanzees produced significantly more visual gestures when the experimenter could see them than when he/she could not, even when the experimenter did not have a direct line of gaze to them. Results suggest that chimpanzees, through a possible process of experience projection based on their own prior experience with mirrors, infer that an experimenter looking at the mirror can see them. We discuss our results in relation to the theory of mind hypothesis that chimpanzees understand seeing in others, and we evaluate possible alternative low-level explanations.

Keywords

behaviour reading; chimpanzee; experience projection; line of gaze; perspective taking; seeing; theory of mind

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In a variety of experimental paradigms, chimpanzees have shown remarkable adaptive and flexible responses to others' direct line of gaze (i.e. the spatial relation between an agent's eyes and nonoccluded items in front of the agent's eyes). In gaze-following studies, for example, chimpanzees have been shown to follow the direct line of gaze of conspecifics and humans to distal objects and locations, even around barriers (Bräuer, Call, & Tomasello, 2005; Hattori, Kano, & Tomonaga, 2010; Kano & Call, 2014; Okamoto-Barth, Call, & Tomasello, 2007; Tomasello, Call, & Hare, 1998). In competitive studies, they have been shown to use information about what objects and events are in a competitor's direct line of gaze to predict the competitor's future action (Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001; Hare, Call, & Tomasello, 2006; Kaminski, Call, & Tomasello, 2008; Karg, Schmelz, Call, & Tomasello, 2015; Melis, Call, & Tomasello, 2006). And in gestural communication studies, they have been shown to produce more visual gestures, such as pointing and lip pouting, towards a human with food when the human has a direct line of gaze to them (Bulloch, Boysen, & Furlong, 2008; Hostetter, Cantero, & Hopkins, 2001; Hostetter, Russell, Freeman, & Hopkins, 2007; Leavens, Hostetter, Wesley, & Hopkins, 2004; Liebal, Pika, Call, & Tomasello, 2004).

The common interpretation of these findings is that chimpanzees respond flexibly and adaptively to others' gaze in such a range of different contexts because they understand the underlying and unifying element in these contexts: that an agent 'sees' something (Call & Tomasello, 2008; Hare et al., 2000). By understanding that a competitor sees food, for example, chimpanzees respond adaptively by predicting that the competitor will move to secure the food. By understanding that a human experimenter in a food-sharing context sees them, chimpanzees respond adaptively by increasing their visual gestures towards the experimenter. And by understanding that agents make sudden changes in the direction of their gaze in order to see new and interesting objects, chimpanzees respond adaptively by following another agent's line of gaze to locate new and interesting objects. The hypothesis that chimpanzees have an understanding that other agents can see things, according to this view, offers the most unified and economical explanation of the various flexible and adaptive responses that chimpanzees give to others' gaze cues in a wide range of contexts. We refer to this widely accepted theory-of-mind interpretation of chimpanzees' adaptive and flexible responses to others' gaze cues as the 'seeing hypothesis'.

However, a competing behaviour-reading hypothesis has also been proposed to explain chimpanzees' behaviour in these experiments. According to what we call the 'line of gaze hypothesis', chimpanzees' adaptive and flexible responses to the direct line of gaze of others in different contexts is simply due to their understanding the various environmental and behavioural consequences (rather than the underlying mental significance) that are contingently linked to gaze cues in others (Davidson & Clayton, 2015; Heyes 1998; Lurz, 2009, 2011; Lurz, Kanet, & Krachun, 2014; Lurz & Krachun, 2011; Perner, 2012; Povinelli & Vonk, 2004; Whiten, 2013). The line of gaze hypothesis suggests that chimpanzees understand (likely through a combination of learning and innate processes) that certain types of behavioural and environmental consequences are contingently dependent upon what another agent within a particular context is directly gazing at. If the context is competitive and a competitor has a direct line of gaze to food, then chimpanzees have learned, likely from past experience, that the competitor will move to secure the food. If the context is food

sharing and the human is gazing directly at the chimpanzee, chimpanzees have learned, again likely from past experience, that visual gestures are an effective means to get the human to share food. And if the context is that of gaze following, and an agent suddenly changes the direction of its gaze, chimpanzees have learned (or perhaps innately know to some degree) that there is likely a new and interesting object at the end of the agent's line of gaze. None of this knowledge of the contingencies between behavioural and environmental consequences and gaze cues in others requires chimpanzees to understand anything about seeing, however.

Some researchers argue that the line of gaze hypothesis, although consistent with the results of the various studies mentioned above, can be ruled out on the theoretical grounds that it requires chimpanzees to know an implausibly large number of distinct behaviour rules (Call & Tomasello, 2008). Other researchers, however, recommend providing stronger support for the seeing hypothesis by ruling out the line of gaze hypothesis on empirical grounds with test procedures that successfully dissociate the variables of seeing and line of gaze (Davidson & Clayton, 2015; Heyes, 1998; Lurz, 2009, 2011; Lurz et al., 2014; Povinelli & Vonk, 2004; Whiten, 2013). The 'goggles' test was specifically designed to achieve this dissociation (Heyes, 1998). In this test paradigm, chimpanzees are first given self-experience with special screens ('goggles') that manipulate whether they can or cannot see things. They are then tested on whether they understand that other individuals wearing or looking at these screens can or cannot see things. At present, three versions of the goggles test have been administered to chimpanzees: an attention-getting version (Vonk & Povinelli, 2011), a gaze-following version (experiment 1 in Karg et al., 2015) and a competitive version (experiment 2 in Karg et al., 2015). However, only the competitive version has yielded positive results. In the familiarization phase of the test, chimpanzees ($N=18$) were given self-experience with two different kinds of screens. One screen was completely opaque when viewed from any angle; another screen (a mesh) was transparent when viewed straight-on but opaque when viewed obliquely. In experimental trials, chimpanzees were presented with a human competitor facing a pair of screens from an angle that made one of the screens transparent to the competitor but the other opaque (although both screens were opaque from the chimpanzee's point of view). The experimental question was whether the chimpanzees would prefer to steal the food behind the opaque or transparent screen. Chimpanzees were found to steal food significantly more often from under the opaque screen than from under the transparent screen. Karg et al. (2015) argued that, given the design of their test, the results could not be explained by any lower-level hypothesis, such as the line of gaze hypothesis, but could be explained by the seeing hypothesis that 'chimpanzees successfully used their self-experience to infer what the competitor sees' (page 211).

Despite the enthusiasm that has been expressed for the goggles test as a method capable of dissociating seeing and line of gaze, some researchers (Lurz, 2009; Perner, 2012) have argued that the test is no better at dissociating these variables than previous experimental paradigms. To appreciate the argument, a few words of clarification are in order regarding the important distinction between seeing and direct line of gaze. As noted earlier, direct line of gaze is a spatial relation that exists between an agent's eyes and nonoccluded objects in front of the agent's eyes. The wall in front of your face is in your direct line of gaze, for example, but the room behind the wall is not, because the wall occludes the room behind it.

Seeing, on the other hand, is not a spatial relation but a state of visual knowledge (Palmer, 1999). That seeing and direct line of gaze are distinct can be easily demonstrated by the fact that there are many things that are in one's direct line of gaze that one does not or cannot see, either because they are too small or far away (e.g. pollen and distant galaxies), camouflaged (e.g. the octopus on the coral), or one's visual system is physically insensitive to them (e.g. ultraviolet light, perfectly polished panes of glass, distant objects for nearsighted individuals). Computing another's direct line of gaze requires determining what nonoccluded objects are in front of the agent's eyes. When the nonoccluded object is one's own face, the computation takes the form of simply noticing that an agent is gazing at you. However, when the nonoccluded object is a distal object, the computation may take on different forms. In some cases, it may require tracing a path in space between the distal object and the agent's eyes. In other cases, where one cannot currently see the distal object, it may require determining the agent's line of gaze based on an analogy to one's own previous line of gaze. One might, for instance, infer that someone currently looking through a crack in a wall has a direct line of gaze to the garden on the other side, based on the fact that when one looked through the crack earlier, one had a direct line of gaze to the garden. Whatever form the computation of another's line of gaze takes, however, its conclusion is always about a particular spatial relation, line of gaze, and not about seeing.

With these points in mind, we return to the argument against the goggles tests as an effective method of dissociating seeing and line of gaze. Central to the argument is the fact that transparent screens are simply not occluders and, therefore, do not prevent an agent's line of gaze. Transparent screens do not prevent one from having a direct line of gaze to objects on the other side of the screen any more so than a crack in a wall prevents one from having a direct line of gaze to objects on the other side of the wall. Thus, in the familiarization phase of the competitive goggles test, it is quite possible that chimpanzees learned that the transparent screen, when viewed straight-on, afforded (like a crack in a wall) a direct line of gaze to items behind it whereas the opaque screen when viewed from the same angle did not. Armed with this knowledge of the different affordances of the screens, chimpanzees could pass the competitive version of the goggles test simply by computing by analogy what the competitor had or did not have a direct line of gaze to, rather than what the competitor could or could not see. Because transparent screens do not dissociate seeing and line of gaze, it is argued, the goggles test fails to be an effective test procedure for empirically ruling out the line of gaze hypothesis.

We propose here an alternative test procedure that more effectively dissociates seeing and line of gaze. A principal difference between our test procedure and the goggles test is that our procedure uses an apparatus that is known to dissociate seeing and line of gaze, a mirror. By looking into a mirror, one sees things, such as one's eyes and the back of the room, to which one does not actually have a direct line of gaze (because these items are not in front of one's eyes). In addition, because chimpanzees are known for their ability to use mirrors to see parts of their bodies to which they lack a direct line of gaze (Gallup, 1970; Mahovetz, Young, & Hopkins, 2016; Povinelli, Gallup, Eddy, Bierschwale, Enstrom, Perilloux, & Toxopeus, 1997), mirrors are an ideal way to test chimpanzees' understanding of seeing with a method that dissociates seeing and line of gaze. In the current study, we tested chimpanzees in a gestural communication paradigm similar to that used in Hostetter et al.

(2007), but we included a mirror. We investigated chimpanzees' frequency of producing visual gestures in the presence of a human experimenter who could see them (as a result of looking into a mirror) but who lacked a direct line of gaze to them (as a result of having his/her back and head turned away).

In accordance with the seeing hypothesis, we predicted that chimpanzees would behave similarly when an experimenter was turned away and gazing at them in a mirror (and so did not have a direct line of gaze to them) as they would when the experimenter was facing forward and gazing directly at them. Also in keeping with the seeing hypothesis, we further predicted that chimpanzees would produce more visual gestures when the experimenter was gazing at them in a mirror than they would under various conditions in which the experimenter could not see them (for example, because the mirror was turned backwards, or because the experimenter was not present). In contrast to these predictions, the line of gaze hypothesis predicts that chimpanzees should not behave differently when the experimenter is turned away and gazing at them in a mirror than under various conditions in which the experimenter also lacks a direct line of gaze to them. Thus, our goal for this study was to provide stronger empirical support for the seeing hypothesis than previous studies have done by varying an experimenter's direct line of gaze separately from his/her ability to see the chimpanzees.

EXPERIMENT 1

Methods

Participants—Twenty-two adult chimpanzees (6 males, 16 females) from nine separate social groups at the Yerkes National Primate Research Center (YNPRC) participated in experiment 1 (mean $\pm$ SD age = 29.36 ± 9.02 years). Testing was carried out at both the YNPRC's main centre in Atlanta, Georgia, U.S.A., and its field station in Lawrenceville, Georgia. Two of the 22 chimpanzees were wild born and the remaining were raised in captivity. All individuals were grouped in enclosures equipped with indoor/outdoor access, nesting materials and environmental enrichment items (e.g. toys, swinging and/or climbing structures and barrels). Throughout the study, the chimpanzees were fed their regular diet, had water available ad libitum and participated voluntarily in all sessions by approaching the experimenter when called. The YNPRC is accredited by the American Association for the Accreditation of Laboratory Animal Care. All procedures used with the chimpanzees were approved by the Institutional Animal Care and Use Committee of YNPRC (IACUC protocol number: YER- 2001074-041718GA) and were conducted in accordance with the ASAB/ABS's Guidelines for the treatment of animals in behavioural research and teaching. All of the chimpanzees had previously participated in a recent mirror self-recognition study (Mahovetz et al., 2016); however, none of the chimpanzees had ever participated in a gesturing study with mirrors.

Experimental set-up and design—Chimpanzees were tested individually in their regular indoor or outdoor enclosure. At the front of the enclosure, a wire mesh separated the chimpanzee and the experimenter (E). A table ($79 \times 36 \times 48$ cm) with a sliding top was placed approximately 10 cm away from the front of the enclosure, and E sat opposite the

chimpanzee approximately 20 cm behind the table. A large mirror (either 91 × 91 cm or 61 × 91 cm, depending on the testing location) was placed in front of the chimpanzee's enclosure in a standing metal frame. A Canon Vixia HV40 digital video camera was used to record all trials. The camera sat on a tripod approximately 2 m away from the front of the chimpanzee enclosure and was aimed directly at the front of the enclosure.

There were five test conditions (see Procedure). Each chimpanzee received two separate experimental sessions consisting of five trials each, one trial for each condition. A small number of trials was run in order to avoid the distorting effects of learning. Specifically, we were concerned that repeated trials in which the experimenter sat still for 2 min without responding would teach chimpanzees that it was fruitless to gesture, even when the experimenter could see them. The chimpanzees might then fail to show the differences across conditions that we expected to spontaneously occur in response to the experimental manipulations. Our reason for not responding to chimpanzees' gestures was to avoid potential learning effects. Povinelli and Eddy (1996) found that chimpanzees quickly learned to respond to novel body cues of an experimenter within just a few differentially rewarded trials, and we wanted to avoid this sort of learning effect. To minimize order effects, the order of conditions was randomized across participants within each session, with the constraint that each condition had to occur an approximately equal number of times in each position.

Procedure—At the beginning of every trial, the mirror was placed behind the table with its reflective side facing the enclosure. For a brief period (typically, 1–2 min), E engaged with the chimpanzee by calling his/her name and pointing at the mirror. This allowed the chimpanzee to become familiar with the mirror so that any initial reaction to its presence would be less likely to influence the outcome of the trial. Following this pretrial exposure, E fed the chimpanzee three pieces of food (e.g. grapes) one at a time from a clear plastic bowl filled with food. E then set the bowl of food in the centre of the table, directly in front of the chimpanzee but out of reach, and proceeded to administer one of the following five conditions.

Face Forward: The nonreflective side of the mirror was oriented towards the chimpanzee. E sat down directly facing the front of the enclosure and gazed directly at the chimpanzee's face without moving for 2 min (see Fig. 1a). At the end of the 2 min, E gave the chimpanzee a piece of food from the bowl (this was done in every condition).

Mirror Forward: The reflective side of the mirror was oriented towards the chimpanzee. E sat down with his/her back to the enclosure and looked at the image of the chimpanzee's face in the mirror for 2 min (see Fig. 1b).

Mirror Away: The nonreflective side of the mirror was oriented towards the chimpanzee. E sat with his/her back to the enclosure and gazed at the nonreflective side of the mirror for 2 min (see Fig. 1c).

Face Picture: The nonreflective side of the mirror was oriented towards the chimpanzee. Before sitting down, E taped a life-sized colour photograph (8.5 × 11 inches, 22 × 28 cm) of

his/her face (head and neck) with eyes open to the nonreflective side of the mirror facing the chimpanzee (see Fig. 1d). Thus, the chimpanzee could see a photo of E's face in approximately the same location as E's reflection would be in the Mirror Forward condition. We ran this condition to test for the possibility that an increase in visual gestures in the Face Forward and Mirror Forward conditions was simply due to the chimpanzees seeing E's eyes, either directly or in an image, without any understanding that those eyes could see them. Because chimpanzees are well known for their ability to see and recognize human and conspecific eyes and faces in photos (Boysen & Berntson, 1986, 1989; Kano & Tomonaga, 2008; Parr & de Waal, 1999; Parr, Winslow, Hopkins, & de Waal, 2000; Taubert, Weldon, & Parr, 2017; Tomonaga & Imura, 2010), we presented the chimpanzees with a photo of E's face that was similar in size, colour, location and orientation as the mirror image of E's face in the Mirror Forward condition. To make the photo as similar as possible to the mirror image, the face depicted in the photo was the same experimenter running the test session, and the clothes and protective garments (e.g. surgical mask and hair covering) the experimenter was wearing in the photo were similar to the ones he/she was currently wearing in the test session (protective garments not shown in Fig. 1). If the chimpanzees simply gestured more when they saw E's eyes directly or in an image, without any understanding of whether or not E could see them, then we would expect equal frequencies of gesturing across all of the Face Forward, Mirror Forward and Face Picture conditions.

Mirror Only: The reflective side of the mirror was oriented towards the chimpanzee. After placing the bowl of food on the table, E exited the testing area, and the chimpanzee was left alone for 2 min (see Fig. 1e). We ran this condition to test for the possibility that an increase in visual gestures in the Mirror Forward condition relative to the other conditions could have been due to the chimpanzees gesturing at their own mirror image.

Figure 1 depicts the five conditions used in experiment 1. Table 1 lists the different variables, along with the mean number of gestures, for each condition in experiment 1 and experiment 2.

Behaviour ethogram and coding—All experimental trials were videorecorded and coded later by one primary coder (R.L.) for visual gestures. For the purposes of this study, a 'visual gesture' was defined as any behaviour that did not produce an obvious sound and that chimpanzees are known to use in a variety of circumstances in an apparent attempt to request food or gain attention from experimenters or conspecifics. We focused on types of visual gestures that have been identified in previous research as species-typical visual attention-getting behaviours (see Table 2). In addition, because chimpanzees are known to have idiosyncratic forms of visual communicative gestures (Roberts, Roberts & Vick, 2014; Tomasello, Call, Nagell, Olguin & Carpenter, 1994), we included an 'other' category to capture visual gestures that appeared to be for attention getting but were not classifiable into any of the other six species-typical categories (only 4% of visual gestures fell into this category for both experiments). To avoid an overly wide range of visual gestures, we excluded all visual gestures that were not typically associated with begging or attention getting (such as scratching, self-grooming or licking the cage mesh). The visual gestures of each chimpanzee during each 2 min trial were classified according to an ethogram of seven

behavioural categories: pointing, bartering, presenting, lip pout, spitting, facial display and other (see Table 2).

For interrater reliability, 20% of trials from experiment 1 (45 trials) were pseudorandomly selected with the stipulation that an approximately equal number of trials from each condition be included in the selection. In addition, 20% of the trials from experiment 2 below, which amounted to five trials, were also included in the reliability coding. Thus, a total of 50 trials were coded from the videotapes for reliability. An independent coder who was naïve to the hypotheses being tested, and who also could not see the orientation of the mirror in the videos, coded these 50 trials for visual gestures according to the ethogram in Table 2. The reliability coder was instructed to count every instance of each of these behaviours observed. Because of the inherent difficulty of video coding the behaviour of chimpanzees, as they move quite quickly and often produce multiple gestures in rapid succession, we did not expect to find perfect agreement between raters in the absolute number of behaviours observed. For example, one coder might spot what he/she believed to be six clear instances of pointing during a 2 min trial, while a second coder might spot only five such instances. What was more important than absolute agreement was that the coders agreed on the relative number of visual gestures made across conditions (i.e. both coders agreed well on which conditions elicited relatively more or fewer gestures). Nevertheless, we did measure both the absolute and relative agreement across coders to get a fuller picture of their agreement.

The absolute number of behaviours coded by the reliability coder agreed reasonably well with the main coder's. The average difference in the number of visual gestures detected by each coder in a given video was just 1.02, and the median difference was 0. Cohen's Kappa calculated on these trials also indicated moderate agreement at $k = 0.436$ (two-tailed $P < 0.001$). More importantly, however, the raters agreed on the relative number of gestures occurring across conditions, which is appropriately measured by the intraclass correlation coefficient (ICC) (Shrout & Fleiss, 1979). The ICC for our data was 0.895 (two-tailed $P < 0.001$), indicating high agreement between raters in the relative number of behaviours produced by the chimpanzees across conditions.

Results

Initial visual inspection of the distribution of scores within each condition indicated that the data were positively skewed, as a greater proportion of scores occurred in the lower range than in the higher range. This was confirmed by two-tailed Shapiro–Wilk tests ($P < 0.05$) for all conditions, with the exception of the Mirror Forward condition ($P = 0.282$). Because of the positive skew for most conditions and the relatively small sample size in both experiments, nonparametric tests were used. All analyses were two-tailed and the significance criterion value was set at $P < 0.05$.

Figure 2 shows the mean number of visual gestures produced by the chimpanzees in each of the five conditions. We first conducted a Friedman test to determine whether there were significant differences across the five conditions in the number of visual gestures produced by the chimpanzees. The test indicated that the response rates did differ across conditions ($\chi^2_4 = 41.18$, $P < 0.001$). We then conducted paired comparisons to determine whether the

pattern of results across conditions was consistent with the seeing hypothesis, as predicted. Because the paired comparisons were not excessive in number, were planned in the design of the study and were all complementary ways of testing the main hypothesis (rather than being independent hypotheses), alpha corrections were not deemed necessary.

Results from the paired comparisons showed that the greatest number of visual gestures occurred in the Face Forward condition, and this condition elicited significantly more gestures than any of the other four conditions (see Table 3). Given that the experimenter could see the chimpanzee in both the Face Forward and Mirror Forward conditions, the significant difference between those conditions did not support the seeing hypothesis, contrary to our predictions. On the other hand, a comparison of the Mirror Forward condition to the three nonseeing conditions (Mirror Away, Face Picture, Mirror Only) did support the seeing hypothesis, as chimpanzees produced significantly more gestures in the Mirror Forward condition than in all three nonseeing conditions. In addition, the only significant difference across the three nonseeing conditions was between the Face Picture and Mirror Only conditions. Thus, gesturing was significantly lower across the three nonseeing conditions than in the two conditions in which the experimenter could see the chimpanzee (Face Forward and Mirror Forward). The one significant difference that was observed between the Face Picture and Mirror Only conditions was likely due to the fact that gesturing in the latter was extremely low (fewer than two gestures in 2 min, on average) whereas the Face Picture condition had the highest mean across the three nonseeing conditions (although still significantly lower than in both of the seeing conditions).

In summary, the pattern of results in the Mirror Forward, Mirror Away, Face Picture and Mirror Only conditions showed that chimpanzees were gesturing more when the experimenter could actually see them, and they were not just gesturing in response to a face/eye stimulus or their own mirror image. Below, we discuss our findings and give a possible reason why chimpanzees failed to gesture equally in both the Face Forward and Mirror Forward conditions, despite gesturing more in the Mirror Forward condition relative to the three nonseeing conditions.

Discussion

In experiment 1, we adapted Hostetter et al.'s (2007) gestural communication study by using a mirror in the critical test condition (Mirror Forward) to create a situation in which an experimenter could see the chimpanzees without having a direct line of gaze to them. If the line of gaze hypothesis were correct, chimpanzees should have treated the Mirror Forward condition like the other conditions in which the experimenter did not have a direct line of gaze to them (i.e. the Mirror Away, Face Picture and Mirror Only conditions) and produced the same number of visual gestures in all four conditions. However, our findings showed that the chimpanzees did not, in fact, treat all of these conditions equally. Instead, as predicted by the seeing hypothesis, the chimpanzees produced significantly more visual gestures in the Mirror Forward condition than in each of three conditions in which the experimenter could not see them. This pattern of results rules out the line of gaze hypothesis and leaves the seeing hypothesis as the more plausible account of our data. Results from the Mirror Forward and Mirror Away conditions showed that the chimpanzees spontaneously

discriminated between an experimenter whose body was turned away but whose face could be seen (in the mirror) and an experimenter whose body was turned away but whose face could not be seen. It is of interest to note that these results are inconsistent with Povinelli and Eddy's (1996) well-known study (experiment 3, condition C'') in which chimpanzees failed to spontaneously discriminate between an experimenter whose body was turned away but whose face (turned forward) could be seen, and an experimenter whose body was turned away and whose face (turned away) could not be seen. It is possible that the inability of the chimpanzees in Povinelli and Eddy's study to discriminate these conditions was due to their immature age (all subjects were between 5 and 6 years of age).

In addition, in the present study, the experimenter's eyes and face could be seen directly (in the Face Forward condition) and in an image (in both the Mirror Forward and Face Picture conditions). However, our results showed that the chimpanzees gestured significantly less when presented with the experimenter's eyes in the photo (when the experimenter could not see them) than when they were presented with the experimenter's eyes in the mirror or directly (when the experimenter could see them). These results make it unlikely that chimpanzees simply increased their visual gesturing when presented with an experimenter's eyes directly or in an image, once again leaving the seeing hypothesis as the more plausible account. The results from experiment 1, therefore, provide evidence that chimpanzees modulate their visual gestures depending on whether they think an agent can see them, not simply on whether an agent has a direct line of gaze to them, or on whether they can see an agent's eyes directly or in an image. It is important to clarify that the seeing hypothesis does not claim that chimpanzees understand seeing as an internal psychological process (indeed, philosophers and scientists debate whether seeing is such a process, see Gibson, 2014; Noë, 2004); rather, the hypothesis claims only that chimpanzees understand seeing as a state of knowledge that is distinct from the spatial relation of direct line of gaze.

Contrary to our expectations, the chimpanzees did not produce similar numbers of visual gestures in the two conditions in which the experimenter could see them (the Face Forward and Mirror Forward conditions). In addition, the amount of gesturing in the Mirror Forward condition, although significantly greater than in the nonseeing conditions, was more like the latter conditions than the Face Forward condition. We suggest that the difference between the Face Forward and Mirror Forward conditions could have been due to the different body orientation of the experimenter in these two conditions. In only the Face Forward condition was the experimenter's body (torso, arms and legs) oriented towards the chimpanzee. In their gestural communication study, Kaminski, Call, and Tomasello (2004) found that apes directed significantly more attention-getting behaviours to an experimenter whose body was oriented towards them ('front face' condition) than to one whose body was oriented away from them ('back face' condition), even though the experimenter could see the apes in both conditions. According to these researchers, the reason the apes produced more attention-getting behaviours in the front face condition than the back face condition was that they interpreted a forward-facing human as having a greater capability of transferring food than a backward-facing human. It is possible, then, that the chimpanzees in our study were more inhibited in producing gestures in the Mirror Forward condition than in the Face Forward condition because they believed that the experimenter (on account of his/her body orientation) was less capable of delivering food in the former condition than in the latter

condition. This significant reduction in gesturing in the Mirror Forward condition would also explain why the results of the Mirror Forward condition were more like those observed in the nonseeing conditions (in which the experimenter also lacked a forward-facing body) than in the Face Forward condition. Note, however, that the forward-facing body of the experimenter in the Face Forward condition would not explain the significant, albeit smaller, differences between the Mirror Forward condition and the three nonseeing conditions (in all of which the experimenter lacked a forward-facing body). Rather, the difference in gesturing between the Mirror Forward condition and the three nonseeing conditions was, as the seeing hypothesis predicts, likely due to the chimpanzees understanding that the experimenter could see them in the former condition but not in the latter conditions. Thus in experiment 2, we tested the hypothesis that the difference in gesturing observed in the Face Forward and Mirror Forward conditions was due to the difference in the experimenter's body orientation by holding the experimenter's body orientation constant (forward facing) while varying only his/her ability to see the chimpanzee.

EXPERIMENT 2

Because we could not rule out that our chimpanzees gestured less in the Mirror Forward than in the Face Forward condition of experiment 1 as a result of the experimenter's differential body orientation, we held body orientation constant in experiment 2 while varying only the experimenter's ability to see the chimpanzee. Specifically, we had the front of the experimenter's body (torso, arms and legs) oriented towards the chimpanzee in three conditions: Face Forward, Over-the-shoulder Mirror Forward and Over-the-shoulder Mirror Away conditions (Fig. 3). In the latter two conditions, the experimenter was gazing over his/her shoulder at the mirror, which was turned either towards or away from the chimpanzee's enclosure. If chimpanzees produced an equivalent number of gestures in the Face Forward and Over-the-shoulder Mirror Forward conditions but significantly fewer gestures in the Over-the-shoulder Mirror Away condition, this would provide clearer support for the seeing hypothesis.

Methods

Participants—Thirteen adult chimpanzees (4 males, 9 females) at the Yerkes National Primate Research Center (YNPRC) participated in experiment 2 (mean $\pm$ SD age = 25.8 $\pm$ 5.0 years). Nine of these chimpanzees had also participated in experiment 1, and all were raised in captivity. Testing was carried out at both the YNPRC's main centre in Atlanta, Georgia, and at its field station in Lawrenceville, Georgia, and involved four separate social groups. Housing and testing conditions for all participants, as well as ethical guidelines and IACUC approval, were the same as described in experiment 1. All the chimpanzees had previously participated in a mirror self-recognition study (Mahovetz et al., 2016); however, none had ever participated in a gestural communication study in which a human experimenter sat with his/her body facing the subject while his/her head was turned away from the subject.

Experimental set-up and design—The experimental set-up was the same as in experiment 1. However, experiment 2 included just three experimental conditions: the Over-

the-shoulder (OTS) Mirror Forward condition, OTS Mirror Away condition and Face Forward condition (see Procedures). All chimpanzees received one trial each of the OTS Mirror Forward and OTS Mirror Away conditions within the same session, in counterbalanced order. One trial of the Face Forward condition was administered to only those four chimpanzees who had not participated in experiment 1 (as we already had the Face Forward data for the individuals who had participated in experiment 1, and we could use the first trial from that data for those chimpanzees). For those four chimpanzees, the Face Forward condition was run in a separate session at least 48 h before the other two conditions.

Procedure—As in experiment 1, each trial was preceded by a mirror-familiarization period in which the mirror was placed behind the table with its reflective side facing the enclosure. E engaged with the chimpanzee during this period by calling his/her name and pointing at the mirror for approximately 1–2 min. Following this pretrial exposure, E fed the chimpanzee three pieces of food one at a time from a clear plastic bowl filled with food. E then set the bowl of food in the centre of the table, directly in front of the chimpanzee but out of reach, and administered one of the following conditions.

Over-the-shoulder Mirror Forward: The reflective side of the mirror was oriented towards the chimpanzee. E sat down facing the chimpanzee and (while keeping torso, arms and legs facing forward) looked over his/her shoulder at the image of the chimpanzee's face in the mirror for 2 min (see Fig. 3a). At the end of the 2 min, E gave the chimpanzee a piece of food from the bowl (this was done in every condition).

Over-the-shoulder Mirror Away: The nonreflective side of the mirror was oriented towards the chimpanzee. E sat down facing the chimpanzee and looked over his/her shoulder and gazed at the nonreflective side of the mirror for 2 min (see Fig. 3b).

Face Forward: As noted earlier, this condition was run only with those chimpanzees who had not participated in experiment 1. It was identical to the Face Forward condition of experiment 1 except that only one trial was run instead of two (see Fig. 3c).

Behaviour ethogram and coding—All experimental trials were videorecorded and then coded later by one primary coder (R.L.) for visual gestures. The behaviours of each chimpanzee during each 2 min trial were classified according to the same ethogram of seven behaviours used in experiment 1 (see Table 2). For information on interrater reliability, see the Behaviour ethogram and coding section for experiment 1 above.

Results

As in experiment 1, the data were positively skewed in the Face Forward and Mirror Away conditions (Shapiro–Wilk tests: $P = 0.05$) but not in the Mirror Forward condition ($P = 0.722$). As before, we ran nonparametric analyses with a significance criterion value of $P < 0.05$ (two tailed).

Figure 4 summarizes the results of experiment 2. As predicted, the chimpanzees produced significantly more visual gestures in the OTS Mirror Forward condition in which E could see

them than in the OTS Mirror Away condition in which E could not see them (see Table 4). Having E's body oriented forward in experiment 2 also meant that the OTS Mirror Forward condition was now more similar to the Face Forward condition of experiment 1 than the original Mirror Forward condition had been in experiment 1. This would lead us to expect the chimpanzees' behaviour in the OTS Mirror Forward condition to now be more similar to their behaviour in the Face Forward condition than we had previously observed. To investigate this possibility, we compared the number of visual gestures produced by chimpanzees in the OTS Mirror Forward condition and the Face Forward condition. (Recall that the data for the Face Forward condition came from the first session of experiment 1 for nine of the chimpanzees.) As reported in Table 4, there was now no significant difference in the number of visual gestures produced by the chimpanzees across the Face Forward and OTS Mirror Forward conditions. Furthermore, when comparing the Face Forward condition with the OTS Mirror Away condition, we found that the chimpanzees produced significantly fewer visual gestures in the latter. Thus, when E's body was oriented forward, the chimpanzees reliably produced a greater number of visual gestures when E could see them (i.e. when E's face was also oriented forward, or when E was looking over his/her shoulder into a mirror) than when E could not see them.

Discussion

In experiment 2, we tested the effect of body orientation on the chimpanzees' ability to discriminate between when E could see them and when he/she could not see them. Our results showed that, when E's body was oriented forward, the chimpanzees behaved exactly as the seeing hypothesis predicted, producing similar numbers of visual gestures across conditions in which E could see them (Face Forward and OTS Mirror Forward), but significantly fewer in the condition in which E could not see them (OTS Mirror Away). In addition, because E did not have a direct line of gaze to the chimpanzees in either the OTS Mirror Forward or OTS Mirror Away conditions, the line of gaze hypothesis cannot predict or explain the significant difference in the visual gestures observed across these two conditions.

GENERAL DISCUSSION

Findings from a variety of gaze following, food competition and gestural communication studies, in conjunction with theoretical arguments, have made the seeing hypothesis (chimpanzees understand that others see) very plausible (Call & Tomasello, 2008). However, none of these studies has been successful in experimentally ruling out the competing line of gaze hypothesis. Our study aimed to do this by investigating the frequency of chimpanzees' visual gestures towards a human experimenter who could see them (as a result of looking into a mirror) but who lacked a direct line of gaze to them (as a result of having his/her head turned away). The results of our two experiments show that chimpanzees distinguish between experimenters who can see them (regardless of whether or not they have a direct line of gaze to them) and experimenters who cannot see them. The results are predicted and explained by the seeing hypothesis but not by the line of gaze hypothesis. In addition, results from experiment 1 show that chimpanzees do not increase their gesturing simply when they

are presented with the experimenter's eyes directly or in an image but, as the seeing hypothesis predicts, only when the experimenter's eyes can see them.

The line of gaze hypothesis is a well-known and significant low-level alternative to the seeing hypothesis; however, it is not the only low-level alternative to the seeing hypothesis. Here we consider two other possible low-level explanations. Direct line of gaze, as noted above, is a spatial relation that exists between an agent's eyes and nonoccluded objects in front of the agent's eyes. Thus, in those conditions in which the chimpanzee is not in front of the experimenter's eyes, such as when experimenter's head is turned away, the experimenter does not literally have a direct line of gaze to the chimpanzee. However, it may be suggested that, in the Mirror Forward condition, at least, the experimenter does have what might be called a 'mirror-mediated' line of gaze to the chimpanzee (mediated, that is, by a mirror image of the experimenter gazing at the chimpanzee). Thus, it could be argued, what our study shows is that chimpanzees discriminate between mirror-mediated line of gaze and no line of gaze, but that this no more implies they understand the state of seeing than does their ability to discriminate between direct line of gaze and no line of gaze.

Its ingenuity notwithstanding, we do not find this mirror-mediated line of gaze hypothesis to be more plausible than the seeing hypothesis. As already noted, our chimpanzees did not have any experience prior to our tests with a contingency existing between humans feeding them and humans having a mirror-mediated line of gaze to them. Consequently, there is no independent reason to expect that chimpanzees would treat a mirror-mediated line of gaze of an experimenter in a feeding context as either (1) significantly different from no direct line of gaze (as they do in experiments 1 and 2) or (2) as equivalent to direct line of gaze (as they do in experiment 2). Thus, unlike the seeing hypothesis, which has been independently supported by a number of separate studies, and which predicts and explains these results, the mirror-mediated line of gaze hypothesis has no independent support and does not predict or adequately explain these results. Therefore, the hypothesis offers a possible but considerably less plausible explanation of our findings than the seeing hypothesis.

A second low-level alternative is that chimpanzees increase their visual gestures simply when they see the experimenter's eyes/head (either directly or in an image) moving. That is, although we included the Face Picture condition to rule out the possibility that chimpanzees simply responded to an eye stimulus, the picture of the experimenter's face was static. It is possible, however, that chimpanzees could respond to moving, blinking eyes (as seen in a live agent) differently from static eyes, without necessitating that they understanding seeing. Thus, in the Face Forward condition, the chimpanzees could see the experimenter's eyes blinking and head moving slightly; and in the Mirror Forward condition, the chimpanzees could also see these movements reflected in the mirror. In the Face Picture condition, however, the experimenter's eyes and head in the photo were not moving, which could explain why the chimpanzees gestured less in this condition than in the Face Forward and Mirror Forward conditions.

We acknowledge that the results of our study cannot rule out this moving eyes/head hypothesis. However, we believe it is less plausible than the seeing hypothesis, for a number of reasons. Whatever movements the experimenter made with his/her eyes and head during

the sessions were minimal, as he/she was required to keep his/her head as still as humanly possible. Furthermore, there are no studies demonstrating that chimpanzees gesture significantly more towards experimenters who blink or move their head slightly than towards experimenters who do not do so. And there is no independent reason to think that had the experimenter not blinked at all and kept his/her eyes and head perfectly still, that this would have caused the chimpanzees to produce significantly fewer gestures in the Mirror Forward condition. In contrast, the seeing hypothesis has gained support from a number of previous studies and, as a result, is antecedently more plausible than the moving eyes/head hypothesis. To experimentally rule out the moving eyes/head hypothesis, chimpanzees would need to be tested in a condition similar to the Face Picture condition except that the experimenter's eyes and head are represented as moving slightly via a moving image. One idea might be to use a video recording or live feed of the experimenter's face presented on a monitor. A potential problem with this method, however, is that the chimpanzees might well interpret the monitor, with the experimenter's face moving on it while the experimenter is looking directly at it, as a type of mirror. Avoiding this possibility was, in fact, the chief reason we opted to use a still photograph rather than a video of the experimenter's face for this control condition. Nevertheless, finding a practical way to run a video control while avoiding this type of error is desirable, as it could help to definitively rule out the use of behavioural cues by chimpanzees in studies on seeing.

On the reasonable assumption that the seeing hypothesis offers the most plausible explanation of our findings, an outstanding question remains. How would the chimpanzees know that the experimenter could see them when he/she was looking at the mirror? To learn that when others look at mirrors they can see things behind their heads, the chimpanzees would need to have had prior experience with others gazing into mirrors while subsequently behaving as if they could see things behind their heads (for example, by reaching for an object that appears behind them without turning around). Given the rarity of such behaviours, together with our chimpanzees' limited experience with mirrors, it is highly improbable they had ever observed others behaving in this way. Furthermore, none of our chimpanzees had any previous exposure to humans feeding them or behaving in any particular manner while looking into a mirror. Thus, it is unlikely that the chimpanzees had prior knowledge about a contingent relationship between humans responding to their visual gestures while the humans gazed into a mirror. It is also implausible to suppose that chimpanzees somehow innately know that when others look at mirrors, they can see things behind their heads. Although the natural environment in which chimpanzees' ancestors lived surely included bodies of water with reflective surfaces, it is unlikely they would have had much (if any) opportunity to observe others responding to things behind their heads as if they could see them while gazing at these reflective surfaces. Given the scarcity of such observations, it is unlikely that there would have been any selection pressure for these apes to evolve innate knowledge of the correlation between others gazing at reflective surfaces and seeing things behind their heads.

A more plausible suggestion is that the chimpanzees came to know about this correlation from their own personal experience with looking at mirrors. From such experience, the chimpanzees could have learned that they themselves could see things behind their heads (e.g. the floor and the wall at the back of their enclosure) while looking in a mirror. Armed

with this self-knowledge, they could have then inferred that the experimenter was also able to see what was behind his/her head (i.e. the chimpanzee) while looking in the mirror. Such an inference constitutes a type of experience projection, in which an individual uses knowledge about the correlation between a state of perception and an observable cue that it has experienced in its own case as a model to infer such states in others based on similar observable cues (Whiten, 1996). Our suggestion that the chimpanzees used such experience projection to know that the experimenter could see them in the mirror is supported by three recent studies (Karg et al., 2015; Karg, Schmelz, Call, & Tomasello, 2016; Schmelz, Call, & Tomasello, 2013). Each of these studies demonstrated that chimpanzees used self-knowledge of their own preferences and line of gaze capabilities to infer similar preferences and line of gaze capabilities in others. It might be suggested that the experience-projection explanation here could be further tested by giving the mirror perspective-taking test to mirror-naïve chimpanzees. However, a potential problem with running the test with such subjects is that chimpanzees often initially react fearfully and aggressively towards mirrors. Such reactions to mirrors by naïve subjects would likely interfere with their capacity to understand the experimenter's perspective in the Mirror Forward condition, subsequently reducing their rate of visual gesturing and increasing the risk of a false negative result.

Past research suggests that chimpanzees may infer a wide range of mental states in others, including perceptions (Hare et al., 2000; Hare et al., 2006; Melis et al., 2006), knowledge (Hare et al., 2001; Kaminski et al., 2008), intentions (Call & Tomasello, 1998; Call, Hare, Carpenter, & Tomasello, 2004), and perhaps even beliefs (Krupenye, Kano, Hirata, Call, & Tomasello, 2016). However, the mentalistic interpretation of those studies is by no means universally accepted (Penn & Povinelli, 2007; Povinelli & Vonk, 2004; Shettleworth, 2010; Suddendorf, 2013; Wynne & Udell, 2013). A number of researchers have maintained that the only way to know whether other species engage in mental state inference is to design studies that effectively rule out alternative low-level explanations (Heyes, 1998; Perner, 2012; Povinelli & Vonk, 2004; Lurz, 2009, 2011; Lurz et al., 2014; Lurz & Krachun, 2011; Whiten, 2013). The current study is the first to rule out the low-level line of gaze hypothesis in favour of the seeing hypothesis. This finding is important because it can increase our confidence in findings from earlier studies; perhaps chimpanzees were indeed using an understanding of seeing, and not just direct line of gaze, to pass those tests as well.

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References

- Boysen S, Berntson G. Cardiac correlates of individual recognition in the chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology*. 1986; 3:321–324. <http://dx.doi.org/10.1037//0735-7036.100.3.321>.
- Boysen S, Berntson G. Conspecific recognition in the chimpanzee (*Pan troglodytes*): Cardiac responses to significant others. *Journal of Comparative Psychology*. 1989; 3:215–220. <http://dx.doi.org/10.1037/0735-7036.103.3.215>.

- Bräuer J, Call J, Tomasello M. All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology*. 2005; 119:145–154. <http://dx.doi.org/10.1037/0735-7036.119.2.145>. [PubMed: 15982158]
- Bullock M, Boysen S, Furlong E. Visual attention and its relation to knowledge states in chimpanzees. *Pan troglodytes*, *Animal Behaviour*. 2008; 76:1147–1155. <http://dx.doi.org/10.1016/j.anbehav.2008.01.033>.
- Call J, Hare B, Carpenter M, Tomasello M. ‘Unwilling’ versus ‘unable’: Chimpanzees’ understanding of human intentional action. *Developmental Science*. 2004; 7:488–498. <http://dx.doi.org/10.1111/j.1467-7687.2004.00368.x>. [PubMed: 15484596]
- Call J, Tomasello M. Distinguishing intentional from accidental actions in orangutans, chimpanzees, and human children. *Journal of Comparative Psychology*. 1998; 112:192–206. <http://dx.doi.org/10.1037/0735-7036.112.2.192>. [PubMed: 9642787]
- Call J, Tomasello M. Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences*. 2008; 12:187–192. <http://dx.doi.org/10.1016/j.tics.2008.02.010>. [PubMed: 18424224]
- Davidson G, Clayton N. New perspectives in gaze sensitivity research. *Learning & Behavior*. 2015; 44:9–17. <http://dx.doi.org/10.3758/s13420-015-0204-z>.
- Gallup G. Chimpanzees: Self-recognition. *Science*. 1970; 167(3914):86–87. <http://dx.doi.org/10.1126/science.167.3914.86>. [PubMed: 4982211]
- Gibson, JJ. *The ecological approach to visual perception*. New York, NY: Taylor & Francis; 2014.
- Hare B, Call J, Agnetta B, Tomasello M. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*. 2000; 59:771–785. <http://dx.doi.org/10.1006/anbe.1999.1377>. [PubMed: 10792932]
- Hare B, Call J, Tomasello M. Do chimpanzees know what conspecifics know? *Animal Behaviour*. 2001; 61:139–151. <http://dx.doi.org/10.1006/anbe.2000.1518>. [PubMed: 11170704]
- Hare B, Call J, Tomasello M. Chimpanzees deceive a human competitor by hiding. *Cognition*. 2006; 101:495–514. <http://dx.doi.org/10.1016/j.cognition.2005.01.011>. [PubMed: 16412413]
- Hattori Y, Kano F, Tomonaga M. Differential sensitivity to conspecific and allospecific cues in chimpanzees and humans: A comparative eye-tracking study. *Biology Letters*. 2010; 6:610–613. <http://dx.doi.org/10.1098/rsbl.2010.0120>. [PubMed: 20335197]
- Heyes C. Theory of mind in nonhuman primates. *Behavioral and Brain Sciences*. 1998; 21:101–148. <http://dx.doi.org/10.1017/S0140525X98000703>. [PubMed: 10097012]
- Hostetter A, Cantero M, Hopkins W. 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*. 2001; 115:337–343. <http://dx.doi.org/10.1037/0735-7036.115.4.337>. [PubMed: 11824896]
- Hostetter A, Russell J, Freeman H, Hopkins W. Now you see me, now you don’t: Evidence that chimpanzees understand the role of eyes in attention. *Animal Cognition*. 2007; 10:55–62. <http://dx.doi.org/10.1007/s10071-006-0031-x>. [PubMed: 16847659]
- Kaminski J, Call J, Tomasello M. Body orientation and face orientation: Two factors controlling apes’ begging behavior from humans. *Animal Cognition*. 2004; 7:216–223. <http://dx.doi.org/10.1007/s10071-004-0214-2>. [PubMed: 15034765]
- Kaminski J, Call J, Tomasello M. Chimpanzees know what others know, but not what they believe. *Cognition*. 2008; 109:224–234. <http://dx.doi.org/10.1016/j.cognition.2008.08.010>. [PubMed: 18849023]
- Kano F, Call J. Cross-species variation in gaze following and conspecific preference among great apes, human infants and adults. *Animal Behaviour*. 2014; 91:137–150. <http://dx.doi.org/10.1016/j.anbehav.2014.03.011>.
- Kano F, Tomonaga M. How chimpanzees look at pictures: A comparative eye-tracking study. *Proceedings of the Royal Society B: Biological Sciences*. 2008; 276:1949–1955. <http://dx.doi.org/10.1098/rspb.2008.1811>.
- Karg K, Schmelz M, Call J, Tomasello M. The goggles experiment: Can chimpanzees use self-experience to infer what a competitor can see? *Animal Behaviour*. 2015; 105:211–221. <http://dx.doi.org/10.1016/j.anbehav.2015.04.028>.

- Karg K, Schmelz M, Call J, Tomasello M. Differing views: Can chimpanzees do level 2 perspective-taking? *Animal Cognition*. 2016; 19:555–564. <http://dx.doi.org/10.1007/s10071-016-0956-7>. [PubMed: 26852383]
- Krupenye C, Kano F, Hirata S, Call J, Tomasello M. Great apes anticipate that other individuals will act according to false beliefs. *Science*. 2016; 354:110–114. <http://dx.doi.org/10.1126/science.aaf8110>. [PubMed: 27846501]
- Leavens D, Hopkins W. Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology*. 1998; 34:813–822. <http://dx.doi.org/10.1037/0012-1649.34.5.813>. [PubMed: 9779730]
- Leavens D, Hostetter A, Wesley M, Hopkins W. Tactical use of unimodal and bimodal communication by chimpanzees. *Pan troglodytes Animal Behaviour*. 2004; 67:467–476. <http://dx.doi.org/10.1016/j.anbehav.2003.04.007>.
- Liebal K, Pika S, Call J, Tomasello M. To move or not to move: How apes adjust to the attentional states of others. *Interaction Studies*. 2004; 5:199–219. <http://dx.doi.org.ez-proxy.brooklyn.cuny.edu:2048/10.1075/is.5.2.03lie>.
- Lurz R. If chimpanzees are mindreaders, could behavioral science tell? Toward a solution to the logical problem. *Philosophical Psychology*. 2009; 22:305–328. <http://dx.doi.org/10.1080/09515080902970673>.
- Lurz, R. *Mindreading animals: The debate over what animals know about other minds*. Cambridge, MA: MIT Press; 2011.
- Lurz R, Kanet S, Krachun C. Animal mindreading: A defense of optimistic agnosticism. *Mind & Language*. 2014; 29:428–454. <http://dx.doi.org/10.1111/mila.12058>.
- Lurz R, Krachun C. How could we know whether nonhuman primates understand others' internal goals and intentions? Solving Povinelli's problem. *Review of Philosophy and Psychology*. 2011; 2:449–481. <http://dx.doi.org/10.1007/s13164-011-0068-x>.
- Mahovetz L, Young L, Hopkins W. The influence of AVPR1A genotype on individual differences in behaviors during a mirror self-recognition task in chimpanzees (*Pan troglodytes*). *Genes, Brain and Behavior*. 2016; 15:445–452. <http://dx.doi.org/10.1111/gbb.12291>.
- Melis A, Call J, Tomasello M. Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *Journal of Comparative Psychology*. 2006; 120:154–162. <http://dx.doi.org/10.1037/0735-7036.120.2.154>. [PubMed: 16719594]
- Noë, A. *Action in perception*. Cambridge, MA: MIT Press; 2004.
- Okamoto-Barth S, Call J, Tomasello M. Great apes' understanding of other individuals' line of sight. *Psychological Science*. 2007; 18:462–468. <http://dx.doi.org/10.1111/j.1467-9280.2007.01922.x>. [PubMed: 17576288]
- Palmer, S. *Vision science: Photons to phenomenology*. Cambridge, MA: MIT Press; 1999.
- Parr L, de Waal F. Visual kin recognition in chimpanzees. *Nature*. 1999; 399:647–648. <http://dx.doi.org/10.1038/21345>. [PubMed: 10385114]
- Parr L, Winslow J, Hopkins W, de Waal F. Recognizing facial cues: Individual discrimination by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*. 2000; 1:47–60. <http://dx.doi.org/10.1037/0735-7036.114.1.47>.
- Penn D, Povinelli D. 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*. 2007; 362:731–744. <http://dx.doi.org/10.1098/rstb.2006.2023>.
- Perner, J. MiniMeta: In search of minimal criteria for metacognition. In: Beran, M.Brandl, J.Perner, J., Proust, J., editors. *Foundations of metacognition*. Oxford, U.K: Oxford University Press; 2012. p. 94–116.
- Povinelli D, Eddy T. What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*. 1996; 61:i–vi. 1–189. <http://dx.doi.org/10.2307/1166159>. [PubMed: 8795292]
- Povinelli D, Gallup G, Eddy T, Bierschwale D, Enstrom M, Perilloux H, et al. Chimpanzees recognize themselves in mirrors. *Animal Behaviour*. 1997; 53:1083–1088. <http://dx.doi.org/10.1016/anbe.1996.0303>.

- Povinelli D, Vonk J. We don't need a microscope to explore the chimpanzee's mind. *Mind & Language*. 2004; 19:1–28. <http://dx.doi.org/10.1111/j.1468-0017.2004.00244.x>.
- Roberts A, Roberts S, Vick SJ. The repertoire and intentionality of gestural communication in wild chimpanzees. *Animal Cognition*. 2014; 17:317–336. <http://dx.doi.org/10.1007/s10071-013-0664-5>. [PubMed: 23999801]
- Schmelz M, Call J, Tomasello M. Chimpanzees predict that a competitor's preference will match their own. *Biology Letters*. 2013; 9:20120829. <http://dx.doi.org/10.1098/rsbl.2012.0829>. [PubMed: 23193044]
- Shettleworth S. Clever animals and killjoy explanations in comparative psychology. *Trends in Cognitive Sciences*. 2010; 14:477–481. <http://dx.doi.org/10.1016/j.tics.2010.07.002>. [PubMed: 20685155]
- Shrout P, Fleiss J. Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin*. 1979; 86:420–428. <http://dx.doi.org/10.1037/0033-2909.86.2.420>. [PubMed: 18839484]
- Suddendorf, T. The gap: The science of what separates us from other animals. New York, NY: Basic Books; 2013.
- Taubert J, Weldon K, Parr L. Robust representations of individual faces in chimpanzees (*Pan troglodytes*) but not monkeys (*Macaca mulatta*). *Animal Cognition*. 2017; 20:321–329. <http://dx.doi.org/10.1007/s10071-016-1054-6>. [PubMed: 27864643]
- Tomasello M, Call J, Hare B. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour*. 1998; 55:1063–1069. <http://dx.doi.org/10.1006/anbe.1997.0636>. [PubMed: 9632490]
- Tomasello M, Call J, Nagell K, Olguin R, Carpenter M. The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates*. 1994; 35:137–154. <http://dx.doi.org/10.1007/BF02382050>.
- Tomonaga M, Imura T. Visual search for human gaze direction by a chimpanzee (*Pan troglodytes*). *PLoS One*. 2010; 5:e9131. <https://doi.org/10.1371/journal.pone.0009131>. [PubMed: 20161750]
- Vonk, J., Povinelli, D. Social and physical reasoning in human-reared chimpanzees: Preliminary studies. In: Roessler, J., Lerman, H., Eilan, N., editors. *Perception, causation and objectivity*. Oxford, U.K: Oxford University Press; 2011. p. 342–368. <http://dx.doi.org/10.1093/acprof:oso/9780199692040.003.0019>
- Waller B, Dunbar R. Differential behavioural effects of silent bared teeth display and relaxed mouth display in chimpanzees (*Pan troglodytes*). *Ethology*. 2005; 111:129–142. <http://dx.doi.org/10.1111/j.1439-0310.2004.01045.x>.
- Whiten, A. When does smart behaviour reading become mindreading?. In: Carruthers, P., Smith, PK., editors. *Theories of theories of mind*. Cambridge, U.K: Cambridge University Press; 1996. p. 277–292.
- Whiten A. Humans are not alone in computing how others see the world. *Animal Behaviour*. 2013; 86:213–221. <http://dx.doi.org/10.1016/j.anbehav.2013.04.021>.
- Wynne, C., Udell, M. *Animal cognition: Evolution, behavior & cognition*. New York, NY: Pelgrave Macmillan; 2013.

Highlights

- Chimpanzees discriminated seeing from direct line of gaze in a gestural paradigm.
- Seeing and line of gaze were dissociated by a strategically placed mirror.
- Findings supported the seeing hypothesis over the line of gaze hypothesis.

Figure 1.
Five conditions of experiment 1: (a) Face Forward, (b) Mirror Forward, (c) Mirror Away, (d) Face Picture and (e) Mirror Only. Drawings by R.L.

Figure 2.

Mean number ($\pm$ SEM) of visual gestures made by chimpanzees in the various conditions of experiment 1. Bars labelled with different letters are significantly different from one another at $P = 0.05$ (two tailed).

Figure 3.
Three conditions of experiment 2: (a) Over-the-shoulder Mirror Forward, (b) Over-the-shoulder Mirror Away and (c) Face Forward. Drawings by R.L.

Figure 4. Mean number ($\pm$ SEM) of visual gestures made by chimpanzees in the various experimental conditions of experiment 2. Bars with different letters are significantly different from one another at $P = 0.05$ (two tailed). OTS = Over-the-shoulder.

Table 1

Variables and mean number of gestures per condition in experiments 1 and 2

Condition	Mirror reflection is present	E's body is turned towards chimpanzee	Chimpanzee can see E's eyes	E can see chimpanzee	Mean no. of gestures
Face Forward ^{1,2}		•		•	7.34 ¹ , 9.00 ²
Mirror Forward ¹	•			•	3.11
Mirror Away ¹					1.86
Face Picture ¹				•	2.07
Mirror Only ¹	•				1.23
OTS Mirror	•	•		•	6.77
Forward ²					
OTS Mirror		•			
Away ²					3.77

E = experimenter; OTS = Over-the-shoulder.

¹Experiment 1.

²Experiment 2.

Table 2

Ethogram of visual gestures

Gestures	Definition
Pointing	Pushing finger(s) through mesh in direction of table, food or experimenter ^{a,b}
Bartering	Pushing objects (e.g. paper, straw, food) through mesh ^b
Presenting	Presenting rump at front of the enclosure ^b
Lip pout	Presenting protruded lower lip at front of the enclosure ^b
Spitting	Spitting towards front of the enclosure ^b
Facial display	Making open - mouth face (withdrawing corners of mouth without exposing teeth) or grimace face (withdrawing corners of mouth and retracting lips to expose teeth) at front of the enclosure ^c
Other	Visual gesture that does not fit above categories (e.g. silently clapping hands, pushing muzzle against mesh, silently striking mesh with hand or foot) ^d

^aDefinition of behavioural category derived from Leavens and Hopkins (1998).

^bDefinition of behavioural category derived from Hostetter et al. (2007).

^cDefinition of behavioural category derived from Waller and Dunbar (2005).

^dFour per cent of visual gestures in experiments 1 and 2 fell into this category.

Table 3

Wilcoxon signed-ranks test results for all paired comparisons in experiment 1

Comparison	Positive ranks, <i>N</i> (ties)	<i>W</i>	<i>P</i>
FF vs MF	17 (0)	228.00	0.001
FF vs MA	19 (2)	208.00	<0.001
FF vs FP	19 (1)	224.50	<0.001
FF vs MO	20 (1)	226.00	<0.001
MF vs MA	17 (2)	171.50	0.013
MF vs FP	16 (1)	178.50	0.028
MF vs MO	17 (2)	188.00	0.002
FP vs MA	11 (6)	78.50	0.584
FP vs MO	13 (4)	136.00	0.027
MA vs MO	10 (5)	106.50	0.155

FF = Face Forward; MF = Mirror Forward; MA = Mirror Away; FP = Face Picture; MO = Mirror Only. Significant values (two-tailed $P < 0.05$) are shown in bold.

Table 4

Wilcoxon signed-ranks test results for all paired comparisons in experiment 2

Comparison	Positive ranks, <i>N</i> (ties)	<i>W</i>	<i>P</i>
OTS-MF vs OTS-MA	8 (5)	36.00	0.012
FF vs OTS-MF	6 (0)	48.00	0.861
FF vs OTS-MA	10 (0)	76.00	0.033

OTS-MF = Over-the-shoulder Mirror Forward; OTS-MA = Over-the-shoulder Mirror Away; FF = Face Forward. Significant values (two-tailed $P < 0.05$) are shown in bold.