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

Robert Lurz [a, *], Carla Krachun [b], Lindsay Mahovetz [c], McLennon J. G. Wilson [d], William Hopkins [e, f]

[a] Department of Philosophy, Brooklyn College, CUNY, Brooklyn, NY, U.S.A.
[b] Department of Psychology, University of Saskatchewan, Saskatoon, SK, Canada
[c] Department of Psychology, Georgia State University, Atlanta, GA, U.S.A.
[d] Department of Psychology, University of Waterloo, Waterloo, ON, Canada
[e] Neuroscience Institute and Language Research Center, Georgia State University, Atlanta, GA, U.S.A.
[f] Division of Developmental and Cognitive Neuroscience, Yerkes National Primate Research Center, Atlanta, GA, U.S.A.

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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.

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, & Tomasello, 2001; Hare, Call, & Tomasello, 2006; Hare, Call, Agnetta, & Tomasello, 2000; 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

* Correspondence: R Lurz, Department of Philosophy, Brooklyn College, 2900 Bedford Avenue, Brooklyn, NY 11218, U.S.A..
E-mail address: rlurz@brooklyn.cuny.edu (R. Lurz).

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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; Kanet, & Krachun, 2014; Lurz, 2009, 2011; Lurz, Perner, 2012; Lurz & Krachun, 2011; 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), they are 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