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Distal Communication by Chimpanzees (*Pan troglodytes*): Evidence for Common Ground?

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Abstract

Van der Goot et al. (2014, *Child Development*) proposed that distal, deictic communication indexed the appreciation of the psychological state of a common ground between a signaler and a receiver. In their study, great apes did not signal distally, which they construed as evidence for the human-uniqueness of a sense of common ground. We exposed 166 chimpanzees to food and an experimenter, at an angular displacement, to ask, "Do chimpanzees display distal communication?" Apes were categorized as (a) proximal or (b) distal signalers on each of 4 trials. The number of chimpanzees who communicated proximally did not statistically differ from the number who signaled distally. Therefore, contrary to the claim by van der Goot et al., apes do communicate distally.

Immense theoretical weight has been given to reports of species differences in cognitive abilities between human beings and representatives of our nearest living relatives, the great apes (e.g., Burkart, Hrdy, & van Schaik, 2009; Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Liszkowski, Schafer, Carpenter, & Tomasello, 2009; Povinelli, Bierschwale, & Čech, 1999; Tomasello, 2008; Tomasello, Call, & Gluckman, 1997). In particular, it is widely believed that human children, as young as 12 months of age, have a unique capacity for cooperative behavior and that this putative species-unique cooperative motivation forms a developmental platform for more advanced sociocognitive representations (e.g., Tomasello, 2008). However, to our knowledge, none of the many empirical studies purporting to demonstrate an early-developing and human-unique capacity for understanding social signals actually supports the conclusion that humans, alone, have these capacities.

For example, no researcher who has claimed to report a species difference in socio-cognitive ability between humans and apes has ever matched the humans and apes on their age or life history stage (Bard & Leavens, 2014). Moreover, no claim of a species difference in social cognition between great apes and humans has ever matched the humans and the apes on their task-relevant pre-experimental experiences (Leavens & Bard, 2011; Lyn, 2010; Pedersen, Segerdahl, & Fields, 2009). Typically, the apes tested are captive-born animals, sometimes orphaned from near birth, and their early rearing histories bear little resemblance to those of the humans being directly compared (e.g., Bard, Bakeman, Boysen, & Leavens, 2014; Leavens, 2014; Leavens, Hopkins, & Bard, 2008). Without exception, to our knowledge, every published claim of a species difference between apes and humans in the display and comprehension of simple, deictic signals, like pointing and directed gaze, has compared culturally embedded humans with apes who have been isolated from human cultural conventions (Boesch, 2007;

2012; Bard & Leavens, 2014; Leavens, 2014; Leavens & Bard, 2011; Lyn 2010). Moreover, to our knowledge, no published claim of a species difference in social cognition between apes and humans has ever administered the same procedure to the humans and to the apes. Therefore, if empirical studies supporting claims of human uniqueness in social cognition comprised the only class of scientific evidence available on the question of comparative social cognition, we would be unable to judge whether these alleged differences between humans and apes in socio-cognitive skill were attributable to (a) their different evolutionary histories, (b) their different life history stages, (c) their different rearing environments, (d) their different experimental protocols, (e) other systematic differences in the life experiences of captive apes and typically developing humans, or (f) some combination of these factors.

Interestingly, when apes and humans are matched on some of these chronic confounding variables, no species differences emerge (Leavens, 2004; Leavens, 2014). For example, with respect to matching apes and humans on age (or life history stage), Horowitz (2003) tested human adults on an imitation task and found that they, like adult chimpanzees, tended not to precisely mimic human demonstrators, but to use idiosyncratic means for opening an “artificial fruit” (see Whiten, Custance, Gómez, Teixidor, & Bard, 1996, for a description of this apparatus and procedure; also see Froese & Leavens, 2014, for a new theory of imitation based on these findings). Thomas, Murphy, Pitt, Rivers, and Leavens (2008) exposed human adults to an experimental condition in which the participants were required to find hidden rewards in one of two possible locations, based, in one condition, on an experimenter’s gaze to a fixation point in the same hemispace, but directed above, not directly at, a baited container. In the original study by Povinelli et al. (1999), adolescent chimpanzees performed above chance in this condition, whereas human 3-year-old children performed at chance (i.e., the chimpanzees were more

successful than the children). They interpreted this “species difference” as evidence that the human children, due to their sophisticated reasoning processes, could not relate the experimenter’s gaze to a location at which the experimenter was not directly looking. Thomas et al. (2008) found that young human adults, like the chimpanzees in Povinelli et al. (1999), easily used the experimenter’s cue to find the hidden rewards. In a direct comparison of cognitive development between a human child and a chimpanzee, Kellogg and Kellogg (1933) reported broad similarity between the two subjects in, for example, the initial development of language comprehension, although the child eventually began to rapidly out-pace the chimpanzee in this regard (it should be noted that the human child was 2.5 months older than the ape). Thus, when apes are approximately matched with humans on age, they tend to act more similarly, particularly in the infancy period.

With respect to matching apes with humans on pre-experimental exposure to human cultural conventions, Carpenter, Tomasello, and Savage-Rumbaugh (1995) reported that enculturated great apes (a chimpanzee, *Pan troglodytes*, and two bonobos, *Pan paniscus*) overlapped with 18-month-old human children in mean durations of joint attention episodes, although the animals were not matched to the children on age or procedure. Although the human children communicated declaratively much more than the apes, two of the three enculturated apes displayed declarative signals, whereas none of the three non-enculturated apes did (see Carpenter & Call, 2013, for an apparent retraction of this claim of protodeclarative signaling). Similarly, Lyn, Russell, and Hopkins (2010) found that enculturated apes significantly outperformed non-enculturated apes in their ability to use human pointing cues to find food. Here, the approximation to a human rearing environment produced humanlike levels of performance (see Leavens, 2014, for additional analysis of this finding). Russell, Lyn,

Schaeffer, and Hopkins (2011) matched 20 great apes on their species, their ages, and, with exception of one pair of apes, on sex, and compared the performances of the 10 enculturated apes against the performances of the 10 non-enculturated animals. They found that the enculturated apes significantly outperformed the non-enculturated apes on tests of both physical and social cognition, derived from the Primate Cognitive Test Battery used by Herrmann et al. (2007). Moreover, the enculturated apes displayed similar response profiles to the three-year-old German children used in the original study by Herrmann et al. (2007). Again, approximate matching for pre-experimental experience between apes and humans rendered broadly similar response patterns to the same kinds of cognitive challenges across the two species.

Recently, van der Goot, Tomasello, and Liszkowski (2014) reported that great apes housed at Leipzig Zoo never communicated about food from a distance. They presented a *lean interpretation* of imperative (requestive) pointing, in which the pointing gesture is seen as a kind of abbreviated reach. Given that most children tested in laboratory contexts are restrained in some way (e.g., strapped into high chairs), the lean interpretation of imperative pointing predicts that were the physical constraints removed, the children would simply approach the objects they desire. In contrast, under a *rich interpretation* of imperative pointing, children understand that their gestures influence the attentional focus of an interlocutor. The rich interpretation of imperative pointing predicts that when constraints to locomotion are removed, children who understand the implications of their signaling for the attentional foci of their interlocutors will simply remain in place, relying on the attention-directing properties of imperative signals to achieve their goal. They applied a similar reasoning to the case of great apes who were constrained by cage mesh--if apes had an appreciation of the attention-directing characteristics of their own signaling attempts, then they should, at least sometimes, signal from a distance, rather

than approaching the cage mesh. Ten of the 12 apes in their study approached a location in which both food and an experimenter were situated, and requested the food with gestures from this position, and none of the apes requested the food with gestures from further back in their enclosures, which van der Goot et al. (2014) interpreted as evidence that the apes did not discern the attention-directing aspect of their imperative signaling. In contrast, about half of the 20 human 12-month-old infants in their study pointed without locomoting towards their rewards (toys), and in accordance with their premises, this was taken as evidence that roughly half of the human children in their study appreciated the attention-directing attribute of their imperative signaling.

Van der Goot and colleagues argued that this apparent difference between the apes and the humans signified the possession, by the 12-month-old humans, of a sense of common ground with the experimenters. They claimed that the infants' positional behaviors implicated young infants' appreciation of these requesting contexts as fundamentally collaborative activities "where the motivation to cooperate becomes as important as the motivation to reach an individual goal" (van der Goot et al., 2014, p. 454). Thus, according to van der Goot et al., gesturing at a distance, or *distal* communication is indicative of the appreciation of common ground in the signaler, whereas *proximal* communication is diagnostic of the absence of this appreciation of common ground.

Several aspects of this argument seem problematic to us. First, as van der Goot et al. (2014, p. 454) noted, it is not unreasonable to suppose that the appreciation of common ground must rely, developmentally, on having experiences of collaborative and responsive responses from one's caregivers. Would a child become as reliant upon the helpful motivations of their interlocutors if their experiences had not fostered those expectations? We believe that it remains

ambiguous whether the subset of children who signaled without approaching their desired toys, in their study, did so because they have phylogenetic histories in which an appreciation of imperative signals as having attention-directing led to differential survival or reproductive success (as van der Goot et al. argued) or, alternatively, because they have had sufficient developmental experiences to foster an expectation that their signals will marshal responsive behavior from their caregivers. Conversely, it is ambiguous whether the apes in that study universally approached the referent (or experimenter) before signaling because of their evolutionary histories or because of their developmental experiences--it is implausible that these institutionalized apes have experienced the same level of responsiveness to their imperative signals from human interlocutors that the human children have experienced. This issue is of central importance to researchers interested in the origins of communicative behavior in humans and their nearest living relatives: if apes raised in institutionalized settings respond differently to experimental challenge from human children raised in Western, postindustrial settings, then because their pre-experimental histories differ so radically, it is logically unclear whether that difference is due to differences in phylogeny, ontogeny, or interactions between genes and environment (Bard & Leavens, 2014; Boesch, 2012; Leavens & Bard, 2011; Leavens et al., 2008; Racine, Leavens, Susswein, & Wereha, 2008). Thus, on deductive grounds, the attribution to phylogenetic factors by van der Goot et al. (2014) of the different performances of the apes and the humans in their study cannot withstand the criticism that the apes and the human children were not matched on pre-experimental experiences of common ground with human interlocutors. Second, the argument presented by van der Goot et al. (2014) is tautological: had the apes in that study behaved like the human children, then there would have been no empirical basis for their claim that a psychological state which they termed "appreciation of common ground" exists, let

alone that it influenced the locomotor behavior of those children. Finally, an obvious weakness of the argument by van der Goot et al. (2014) is their implication that because the 10 apes who signaled in their study all approached the experimenter when they gestured, therefore this is a general response characteristic of great apes.

Because we, and others, have repeatedly observed chimpanzees pointing to objects from positions in their enclosures that were relatively distant from those objects, we had reason to further explore whether van der Goot et al.'s findings are representative of this species. For example, distal pointing by bonobos (*Pan paniscus*) was reported by Pedersen et al. (2009) and by Veà and Sabater-Pi (1998). In addition, it has been well-demonstrated that small changes to a procedure can yield substantial differences in results when studying human and nonhuman primates (e.g., Hopkins, Russell, McIntyre, & Leavens, 2013; Lyn, Russell, Leavens, Bard, Boysen, Schaeffer, & Hopkins, 2014; Lyn, 2010; Mulcahy & Hedge, 2012). With only 10 apes responding in their study, it remains open to question whether their findings are generalizable beyond their subset of animals from the Leipzig Zoo. Therefore, we designed a study to determine whether chimpanzees would always approach desirable food before signaling about it, as the findings of van der Goot et al. (2014) would predict, or would, instead, display the kind of mixed pattern of results displayed by the human children in their study, in which some children approached the reward, but other children did not.

We did not attempt to replicate the design of van der Goot et al. (2014) for several reasons. Their human infants were positioned at systematically closer distances to the reward location (.95 and 1.8 meters, in two different experiments), compared to their great apes, who were separated from the reward location by 6 meters. Any attempt to replicate the study, therefore, would have to systematically vary the task administration across these three distances,

because these distance and species effects were confounded factors in the original study (i.e., there is no objective basis to decide whether the reported behavioral differences between the apes and the humans were attributable to the organisms' different evolutionary histories or the radically different physical arrangements). Similarly, the human children in van der Goot et al. were sitting next to the experimenter with no barrier between them, whereas the great apes were separated from the human experimenters by cage mesh. The orientations and positions of the subjects and the two experimenters varied substantially and systematically with species classification, so, again, to replicate the study would have required flexibility in the physical testing environments that was not available to us with our study population. Finally, in the experimental arrangement administered by van der Goot et al. (2014), an experimenter was standing adjacent to the target location, hence it is ambiguous to which of the two experimenters the apes were signaling.

Therefore, we adopted a new procedure, based on established protocols in our laboratory (Leavens & Hopkins, 1998, 2005; Leavens, Hopkins, & Thomas, 2004), designed to render a clear answer to the question, "Do chimpanzees communicate about food from a distance, or do they always approach as closely as they can to the food, before signaling?" Our general tactic was to (a) reduce the number of potential communicative partners (experimenters) to one, to reduce ambiguity about the intended recipient, (b) to separate the referent from the communicative partner with a wide angle, to reduce ambiguity about whether deictic signals were directed at a person or an object, and (c) to approximately match the distance between subjects and the referents with those used with the human children in van der Goot et al. (2014), in order to eliminate distance as a confounding factor. We presented each of 166 chimpanzees four trials in an experimental situation in which an experimenter and desirable food were

presented to the animals at significant angular displacement, so that it was never ambiguous whether their manual gestures and other signals were food-directed or person-directed.

We reasoned that if van der Goot et al. (2014) are correct in their claim that the appreciation of imperative signaling as an attention-directing device is a uniquely human capacity, then all of the chimpanzees should approach the food before signaling about it to an interlocutor, consistent with their lean interpretation of imperative signaling as a psychologically simple, instrumental act. For researchers interested in child development, if we find that chimpanzees, like human children, display a mixed pattern of response--some communicating at a distance, and some moving as close as possible to the food--then this would imply that there are not substantive psychological differences between chimpanzees and younger human children in their imperative communication. This conclusion would hold regardless of the plausibility of the argument that distal signaling implicates the understanding of imperative communication as an attention-directing signal.

Method

Subjects

In total, 166 chimpanzees were tested in two colonies. Subjects were 125 sub-adult and adult chimpanzees housed at The University of Texas MD Anderson Cancer Center (UTMDACC) ranging in age from 13 to 52 years of age ($M = 31.6$ years, $SD = 9.8$), tested between January and June 2014. There were 74 females and 51 males. Within the sample, there were 71 mother-reared, 20 human-reared and 34 wild-caught apes. Subjects in the sample from Yerkes National Primate Research Center (YNPRC) were 41 sub-adult and adult chimpanzees ranging from 10 to 58 years of age ($M = 28.2$ years, $SD = 11.0$), originally filmed between May 2011 and March 2013; these videos were re-coded for the present study between July and

November 2014. There were 29 females and 12 males. In this sample, there were 19 mother-reared, 19 human-reared, and 3 wild-caught apes. On average, our sample was older (combined $M = 30.7$ years, $SD = 10.2$) than the mean 17.7 years reported for the apes in van der Goot et al. (2014), but our range of 10-58 years considerably overlaps their range of 9-35 years. Systematic analyses revealed no differences in propensity to display either initiating joint attention (IJA, defined below) or in triangulated signaling (TRI, defined below) as a function of age class (see Results), therefore any differences that emerge between our sample and that of van der Goot et al. (2014) are unlikely to be attributable to age. Like apes in most captive circumstances, the UTMDACC and YNPRC chimpanzees were fed 2-3 times daily with commercial primate chow, liberally supplemented with fresh fruits and vegetables. Unlike zoo apes, chimpanzees housed in research facilities are not put out on display during the day, but like zoo apes many have night enclosures in which they sleep, ranging in larger corrals during the daytime. Of particular note, like the apes in van der Goot et al., the UTMDACC and YNPRC chimpanzees were significantly older than the human infants in their study, yet, like the human infants in van der Goot et al., and human infants more generally, they frequently encounter desirable items that are outside their reach, and develop tactics for controlling the activities of caregivers apparently to obtain those otherwise unreachable items, for example, through pointing (e.g., Leavens, Hopkins, & Bard, 1996, 2005a, 2008).

Procedure

Prior to testing, each subject was encouraged to separate from their usual social groups, either into their home cages or in familiar runs, depending on the specific circumstances. Testing areas ranged from 5.76 m² to 13.38 m². Interactions between these chimpanzees and

humans, including routine feeding and husbandry, as well as experimental manipulations, typically take place through the cage mesh in these areas of the animals' captive environments; hence, the distances involved in the present study (see below) are more typical of the interactive distances involved in the day-to-day interactions of chimpanzees than the 6.0 meters used in van der Goot et al. (2014). Immediately prior to each trial a human experimenter (E1) was positioned outside the cage mesh at one end of the subject's home cage. After a short period of time, a second experimenter (E2) approached the enclosure and placed a container of preferred food .5 meter outside the subject's home cage, at the end opposite of the position of E1, then E2 immediately left the area, out of visibility of the chimpanzee. The distance between E1 and the food was approximately 1 to 1.5 meters, and the placement of the food signaled the onset of the trial.

During the next 60 seconds, E1 recorded whether or not the chimpanzee signaled to either them or the food and alternated their gaze between the food and E1. Gaze alternation between a social partner and a referent is a widely used and easily operationalized component of intentional communication in humans (Bates, Benigni, Bretherton, Camaioni, & Volterra, 1977; Desrochers, Morissette, & Ricard, 1995; Franco & Butterworth, 1996; Lempers, 1979; Tomasello, 1995), and used to index the social orientation of accompanying communicative behaviour (see, e.g., Bard, 1992; Leavens & Hopkins, 1999; Leavens, Russell, & Hopkins, 2005b; Plooij, 1978, for discussion of its extension to great ape communication). (Although some contemporary researchers write as though such behavioral indices as gaze alternating behavior provide insight into psychological mechanisms, this interpretation is rejected by Leavens--e.g., 2012; Leavens et al., 2005b, 2009; Racine et al., 2008--here, we simply note, following Leavens et al., 2005b, that gaze alternating behavior meets an objective behavioral

criterion for conventional definitions of intentional communication in both apes and humans.) We used an expanded ethogram, compared to van der Goot et al. (2014), because we reasoned that when a chimpanzee stands in front of a human experimenter, directs its hand in a begging posture towards the experimenter, and alternates its gaze between this experimenter and a distant, desirable referent, this is classically triadic communication about a particular entity, and therefore the propensity of these animals to communicate about this food would be underestimated if we arbitrarily recorded only a subset of their triadic communicative repertoires (these repertoires have been described in Leavens & Hopkins, 1998; Leavens et al., 2004, 2005b). When the chimpanzees signaled with gaze alternation, this was recorded as a successful initiation of joint attention (IJA) response (e.g., Mundy, Kasari, & Sigman, 1992). Signaling responses included pointing, cage banging, pushing an object toward the human or food in an apparent barter attempt (Hyatt & Hopkins, 1993), spitting (rare, only 2 occasions), or throwing (also rare, only 1 occasion). In the absence of gaze alternation between the human and the food, presenting a body part or using the feet to signal were not considered communicative responses, for the purposes of this study. Note that the chimpanzee had to be simultaneously signaling to either the food or human while alternating gaze between the two items. These events could not occur in sequence to be considered a successful joint attention event. In other words, signaling to the food or E1, retracting their gesture or stopping their response, and then alternating their gaze was not considered a successful IJA response. In addition, E1 also noted the position of the chimpanzee when they initiated joint attention as either 1) in front of the food (FOOD) or 2) in front of the human (Human). In relation to the coding scheme of van der Goot et al. (2014), like them, we included points, but unlike them, because we separated the food and the experimenter, we had two classes of manual extensions or gestures: points (to food) and hold hand out

(apparently supplicative gestures directed at the experimenter--see Leavens & Hopkins, 1998; Leavens et al., 2004). Van der Goot et al. (2014) reported grabbing of the cage mesh, but we did not see this behavior in the present study. Behaviors coded by us, but not by van der Goot et al. (2014) included cage bangs, bartering attempts, spitting (2 instances) and one instance of throwing.

In addition to IJA, we computed whether the chimpanzee engaged in the more restricted form of IJA that we defined as triangulated signaling (TRI). Triangulated signaling was defined as the chimpanzee positioning themselves either in front of the human or food and signaling to the more distal referent, be it the human or food. Thus, in these particular cases of IJA, the chimpanzees would either position themselves in front of the food and signal to E1 (and not the food) or they would position themselves adjacent to E1 and signal toward the food (and not E1). Lastly, on some trials, the chimpanzees positioned themselves between the food and E1 and signaled to both items while alternating their gaze. These responses were computed as a separate form of triangulation. Thus, TRI included all instances of IJA in which the chimpanzees' manual gestures were directed to the relevant target (food or E1) that was furthest away from its position, plus the few trials in which the chimpanzees positioned themselves between the food and E1 and signaled to both targets.

Each subject received 4 trials which lasted 60 seconds each. There was at least a 4-minute interval between successive trials. All trials were videorecorded at both colonies. There were some slight differences in coding procedure between UTMDACC and YNPRC: at UTMDACC data were recorded live on datasheets by E1 and the videotaped record consulted to resolve uncertainties, when they arose. At YNPRC, all trials were videorecorded and then subsequently coded from these video records by the fourth and fifth authors. Though the subjects lived in

social groups, they were temporarily separated from their groups during testing, as were the apes in van der Goot et al. (2014), and tested in their home cages. The apes' separation from their social groups was voluntary, and trials were to be terminated in the event of any apparent distress, in accordance with our usual policies, but no subjects displayed any apparent distress in this procedure. No attempt was made to record or manipulate the chimpanzees' initial positions in their cages. E1 and E2 were randomized across subjects and trials; these roles were performed by the second and third authors of this paper at UTMDACC and by the fourth and fifth authors at YNPRC.

Analyses and Reliability

All statistical tests were two-tailed, with alpha set to 0.05; chi-squared tests, Fisher's exact test, Kruskal-Wallis tests, and Mann-Whitney tests were used throughout, consistent with the nominal level of measurement. Prior to testing, inter-rater reliability was established using Cohen's kappa. Ten chimpanzees were filmed while being tested and their four-trial performance was independently scored for IJA by these two independent raters, the second and third authors on this paper, who were blind to the hypotheses under test during both filming and later data collection ($n = 40$ observations, 4 trials x 10 chimpanzees) and who served as E1 and E2. These 10 chimpanzees were later tested again in the formal testing protocol. The percentage agreement in IJA ratings was 92.1 percent ($\text{kappa} = .842$), which is considered excellent (Bakeman & Quera, 2011). Note that TRI classifications were computed from the database recording the behavioral constituents of IJA responses (i.e., all instances in which the gestures were directed to the relevant target furthest away from the closest target at which the chimpanzees were positioned were coded as TRI).

Results

Descriptive Performance

In the initial set of analyses, we examined whether there were any systematic colony-based differences in responses. For these analyses, we used the number of trials on which the chimpanzees initiated joint attention (IJA) or a triangulated (TRI) response. There were no differences between the UTMDACC ($n = 125$) and YNPRC ($n = 41$) colonies on the propensity to display IJA ($U = 2469.5$, $p = .601$; UTMDACC: MDN = 2.0, YNPRC: MDN = 2.0) or TRI ($U = 2388.5$, $p = .491$; UTMDACC: MDN = 1.0, YNPRC: MDN = 1.0). In addition, we checked for differences between the two colonies in positional behavior (proximal versus distal positioning), on a trial-by-trial basis. We found no systematic differences in positional behavior, where subjects who displayed IJA were categorized as having taken up positions proximal to the food, or not, between UTMDACC and YNPRC (Trial 1: $\chi^2(1, N = 82) = 0.02$, $p = .894$; Trial 2: $\chi^2(1, N = 98) = 2.11$, $p = .146$; Trial 3: $\chi^2(1, N = 91) = 3.51$, $p = .061$; Trial 4: $\chi^2(1, N = 92) = 0.96$, $p = .328$). Therefore, we combined data across the two colonies for all subsequent analyses.

In a second set of initial analyses, we examined the potential influences of sex and rearing history on performance. The trial-specific and overall data are shown in Tables 1 and 2. Mann-Whitney U tests were used to test the effects of sex, and Kruskal-Wallis tests were used to test for effects of rearing history on the number of trials with IJA and TRI, respectively. No significant effects of sex ($n = 103$ females, $n = 63$ males) on overall IJA responding were found (Mann-Whitney $U = 3167.5$, $p = .793$; females: MDN = 2.0, males: MDN = 2.0). No significant effects of rearing history were found on IJA performance (Kruskal-Wallis $H(2, N = 166) = 4.63$,

$p = .099$; mother-reared: MDN = 2.0, nursery-reared: MDN = 3.0, wild-born: MDN = 2.0).

Similarly, no significant effects of sex on TRI performance were found (Mann-Whitney $U = 3058.0$, $p = .512$; females: MDN = 1.0, males: MDN = 1.0). Finally, no significant effects of rearing history were found on TRI performance Kruskal-Wallis $H(2, N = 166) = 3.04$, $p = .219$; mother-reared: MDN = 1.0, nursery-reared: MDN = 1.0, wild-born: MDN = 1.0). Given the apparent absence of sex or rearing history effects on either IJA or TRI performance, the data were pooled across these subject variables for comparison with van der Goot et al. (2014).

In a third set of preliminary analyses, we examined the influence of subjects' ages on IJA and TRI performance. Although the UTMDACC colony was, on average, about 3 years older than the YNPRC sample (see Method), this difference was not statistically significant ($t(164) = 1.86$, $p = .065$), therefore the two colonies were combined for further analysis. We categorized each chimpanzee as belonging to one of four age classes: (a) Adolescent (8-12 years, $n = 2$), (b) Young Adult (13-20 years, $n = 19$), (c) Mature Adult (21-35 years, $n = 99$), and Elderly (>35 years, $n = 46$); these age classes correspond to those used by Leavens and Hopkins (1998). Systematic chi-square analyses performed for each of the four trials compared these four levels of age class with two levels each of, respectively, IJA and TRI performance (i.e., the chimpanzees either displayed IJA or not, on any given trial, and either displayed TRI or not, on any given trial). There were no systematic effects of age on IJA or TRI performance (IJA: Trial 1: $\chi^2(3, N = 166) = 5.12$, $p = .163$; Trial 2: $\chi^2(3, N = 166) = 0.46$, $p = .926$; Trial 3: $\chi^2(3, N = 166) = 1.64$, $p = .650$; Trial 4: $\chi^2(3, N = 166) = 3.64$, $p = .302$; TRI: Trial 1: $\chi^2(3, N = 166) = 1.36$, $p = .716$; Trial 2: $\chi^2(3, N = 166) = 0.42$, $p = .935$; Trial 3: $\chi^2(3, N = 166) = 1.72$, $p = .633$; Trial 4: $\chi^2(3, N = 166) = 0.98$, $p = .807$).

As is evident in Table 1, on average, chimpanzees initiated joint attention on 57.8% of

the trials with 30.1% producing IJA on all 4 trials (50/166) compared to only 19.3% who never displayed IJA (32/166). A triangulated response was observed less frequently, with chimpanzees, on average, producing this form of joint attention signaling on 31.7% of trials. Of the 166 chimpanzees, only 16 individuals (9.6%) used this form of communication on all 4 trials compared to 74 individuals (44.6%) who never used it (see Table 2).

A reviewer asked whether frequent communicators (IJA on 3-4 trials, $n = 76$) positioned themselves differently with respect to less frequent communicators (IJA on 1-2 trials, $n = 58$). In other words, could it be the case that positioning preferences and propensity to communicate are confounded, in the present study? To answer this question, we calculated an ordinal variable to describe the distance at which the chimpanzees displayed an IJA response. This was the sum of the total distances recorded over all four trials, divided by the number of trials in which subjects displayed IJA. Subjects who positioned themselves at the food on any given trial were coded as "1"; subjects who positioned themselves midway between the food and the experimenter on any given trial were coded as "2"; and subjects who positioned themselves near the human and communicated most distally were coded as "3" (representing the most distal position). The sums over the four trials could range, thus, from 1 (a subject who positioned itself at the food on only one trial and did not otherwise display IJA) to 12 (a subject who positioned itself near the human and displayed IJA on all four trials). This sum was divided by the number of trials in which each subject displayed IJA, to derive a mean ordinal distance. A Mann-Whitney U test comparing infrequent responders (IJA on 1-2 trials) with frequent responders (IJA on 3-4 trials) was not significant ($U = 1913.5$, $p = .178$; infrequent IJA: MDN = 1.00, frequent IJA: MDN = 1.7). Thus, it was not the case that frequent IJA responders displayed a systematically different positioning tactic, compared to less frequent IJA responders.

Gesture Types

Table 3 reports the frequencies and percents of communicative acts displayed by these chimpanzees, by trial number. For relatively rare multiple signal types, here we classified communication acts in accordance with the following hierarchy: Gesture to food > Gesture to experimenter > Other (e.g., if a subject pointed at the experimenter, then pointed at the food, this would be classified as a gesture to the food). Between 42% and 50% of the communicative acts displayed included a manual gesture directed towards the food or the experimenter. Of these, between 46% and 62% were pointing gestures. Other, non-deictic communicative acts comprised between 8% and 9% of the responses, across the four trials. Between 19% and 29% of the chimpanzees pointed to the food; whereas, between 41% and 61% of the chimpanzees displayed "no communication" (which includes apparently communicative signals that were not accompanied by gaze alternation between the food and the experimenter, as well as trials in which the chimpanzees did not engage with the experimenter).

Signaling Positional Effects

To test the hypothesis that chimpanzees always communicated from the position closest to the food, we compared the occurrence of IJA responses as a function of whether the chimpanzee was positioned in front of the food (Food), in front of the human (Exper.), or between these two entities (Middle) using chi-squared tests for each trial. Some individuals changed position in the course of a trial; we coded all subjects in terms of their first signaling position for these analyses. These data are shown in Figure 1. As is evident from Figure 1, there was a substantial preference displayed by these chimpanzees for communicating either in closest

proximity to the food or in proximity to the experimenter, with relatively fewer animals electing to signal from a position midway between the food and the experimenter (Trial 1: χ^2 (2, $N = 82$) = 27.24, $p < .001$; Trial 2: χ^2 (2, $N = 98$) = 23.41, $p < .001$; Trial 3: χ^2 (2, $N = 92$) = 8.86, $p = .012$; Trial 4: χ^2 (2, $N = 93$) = 19.39, $p < .001$). However, when the two distal positions are combined (Exper. + Middle = Distal) and compared to the individuals who moved to proximity with the Food (= Proximal), systematic binomial tests reveal no bias towards either proximal or distal signaling on any trial (Binomial tests, Trial 1: $p = .097$; Trial 2: $p = 1.000$; Trial 3: $p = .142$; Trial 4: $p = 1.000$)(see Figure 2). (The rationale for combining Middle and Exper. signalers for this analysis is that both responses meet the criterion of not approaching as closely as possible to the food.) Because the food is out of reach even when the chimpanzees move to the closest possible physical proximity with it, therefore even the "proximal" signaling we report, here--using the term as van der Goot et al. (2014) did--involves approximately 50 cm. of distance between the chimpanzees and the referents of their communication. Thus, in our study, the apes did not use a tactic of approaching the food either exclusively, as in van der Goot et al. (2014), or even preferentially. The percentages of individuals who were positioned distally, either in front of the human or between the human and the food for Trials 1 through 4, were 40%, 50%, 58% and 50%, respectively. Among these animals that gestured from a distal position, the number (and percentage) of chimpanzees who pointed to the food on Trials 1 through 4 were 8 of 33 (24%), 22 of 49 (45%), 29 of 53 (55%), and 27 of 46 (59%), respectively.

Comparisons with van der Goot et al. (2014)

Van der Goot et al. (2014) reported that of the 10 apes in their study who responded to the experimental challenge, none of them ($n = 0$) gestured from the backs of their cages ("all 10

apes moved as close as possible to the food items behind the cage and requested from there by protruding the hand through the mesh,” van der Goot et al., 2014, p. 450). We categorized all chimpanzees who responded during the present experiment as positioning themselves (a) in front of the food and communicating from there (proximal) or (b) either between the food and the experimenter or in front of the experimenter and communicating from there (distal). Systematic comparisons with van der Goot et al.’s (2014) data reveal that the present sample was significantly more likely than the Leipzig apes to communicate from a position that was not close to the food for all trials (see Figure 2): Trial 1 (Fisher’s exact test, $p = .012$), Trial 2 (Fisher’s exact test, $p = .002$), Trial 3 (Fisher’s exact test, $p < .001$), and on Trial 4 (Fisher’s exact test, $p = .002$). For these comparisons, we compared the 10 apes from Leipzig with 82, 98, 91, and 92 chimpanzees from the present study on Trials 1 through 4, respectively. Thus, the behavior patterns displayed by the Leipzig apes do not seem to match the UTMDACC and YNPRC apes, and therefore, are not generalizable to all populations of captive apes. Moreover, it is clear from Figure 2 that the chimpanzees we studied do not differ in any systematic way from the human babies. Comparing the positional behaviors of their babies in their Experiment 1 ($N = 17$) with our chimpanzees in Trials 1-4, reveals no differences in Trial 1 (Fisher’s exact test, $p = .421$), Trial 2 (Fisher’s exact test, $p = 1.000$), Trial 3 (Fisher’s exact test, $p = .791$), and on Trial 4 (Fisher’s exact test, $p = 1.000$). Similarly, comparing the positional behaviors of their babies in their Experiment 3 ($N = 22$) with our chimpanzees also reveals no differences in Trial 1 (Fisher’s exact test, $p = .808$), Trial 2 (Fisher’s exact test, $p = .815$), Trial 3 (Fisher’s exact test, $p = .341$), and on Trial 4 (Fisher’s exact test, $p = .814$). As is evident from Figure 2, the Leipzig apes were the only group to display a significant preference for proximal vs. distal signaling.

Discussion

In contrast to the chimpanzees and bonobos studied by van der Goot et al. (2014), the chimpanzees at UTMDACC and YNPRC frequently communicated about the food from positions that were not the closest possible position to the food; i.e., they displayed distal pointing. This is consistent with casual observations conducted during our previous research. It is precisely this pattern of not approaching the target as closely as possible by the human children that led van der Goot et al. (2014) to argue that “infants’ imperative pointing is a cooperative communicative act that directs others’ attention within common ground to desired objects, with the expectation that the recipient will do as one wishes” (p. 448). Our finding that chimpanzees frequently do this has considerable relevance to the theoretical claims of van der Goot et al. (2014). Recall that they argued that this kind of distal signaling was (a) unique to humans and (b) diagnostic of the capacity to recognize a common, shared psychological stance in others. With respect to the first claim, our findings clearly demonstrate that distal signaling is not a uniquely human communicative tactic. Across the four trials, anywhere from 38% to 63% of the responding apes chose to communicate from a position other than at the closest approach to the desirable food. We do not know why our sample of great apes differs so much from the Leipzig group, but we note that the distances involved in our study (~1.0 to ~1.5m) were much closer to those used with the human children (.95 to 1.8 m) than the distances administered to the great apes in their study (~6m), and our chimpanzees responded very similarly to both groups of human children in van der Goot et al. (2014) in the display of distal signaling (see Figure 2). This raises the possibility that simple distance may be among the most influential factors controlling the positional concomitants to signaling behavior in both humans and apes. In addition, and in contrast to van der Goot et al., we did not confound the location of an

experimenter and the desired reward. Hence, perhaps it was the presence of the experimenter (E2, in their study) that drew the Leipzig apes so consistently toward the food in their study.

With respect to the second claim, that distal signaling constitutes an index of the capacity of organisms to recognize a state of shared psychological perspective, or common ground, must we now concede this ability to great apes? According to van der Goot et al. (2014), this is precisely the interpretation we should deliver about the chimpanzees at UTMDACC and YNPRC:

the fact that they always move their body as close as possible toward the desired item suggests that apes are using a strategy of enacting their message rather than presuming the message to be within common ground so that directing attention from afar would suffice (van der Goot et al., 2014, p. 450).

Thus, according to van der Goot et al., 2014, distal signaling indexes the presumption that one's signals are understood within a "common ground" that is shared between both signaler and receiver. It is worth noting that the fact that the children in van der Goot et al. (2014) often approached the reward, indeed in proportions comparable to the chimpanzees in the present study (Figure 2), must be construed, based on their argument, as evidence that these children lacked a sense of the common ground in which the experiment was conducted. According to the claim of van der Goot et al., organisms who approach the reward in these triangular experimental contexts (like the majority of their children and like many of our chimpanzees) lack a sense of common ground. This proximal signaling is their index of the absence of common ground in

communicative interactions. Conversely, their behavioral index of the psychological appreciation of a common ground is the distal signaling displayed by many of their children and many of our chimpanzees.

An alternative, arguably simpler explanation for the mixed tactics of approach and non-approach displayed by the infants in van der Goot et al. is simply that their sample of children was composed of children displaying a spectrum of social inhibition (Fox, Henderson, Marshall, Nichols, & Ghera, 2005; Garcia Coll, Kagan, & Reznick, 1984). There are well-described individual differences in approach behavior among humans, so to find that some infants approached the toys, whereas others did not, as van der Goot et al. (2014) reported, is not unexpected. The striking difference between the chimpanzees in the present study and the great apes in van der Goot et al. (Figure 2) is somewhat less amenable to explanation by appeal to temperamental factors. Perhaps there may be systematic differences in the levels of perceived environmental threat between research institutions and zoos, which differentially influence the readiness of these apes to approach humans. Consistent with this conjecture, whereas 17% (2 of 12) of the apes in van der Goot et al. declined to respond to the experimental challenge, in the present study between 41% and 51% (within the four trials) of the chimpanzees declined to engage with the experiment with the display of communicative behavior (Table 3). Thus, at the very least, it seems reasonable to suggest that non-cognitive temperamental and environmental factors might have influenced the patterns of response reported in these two studies.

Without necessarily speaking to the utility of the concept of a common ground in understanding organismic interactions, we argue that this concept is not well operationalized, if the argument is that organisms who display proximal communication lack a concept of common ground or, conversely, that organisms who display distal communication possess this concept.

In summary, according to the argument presented by van der Goot et al. (2014), many of our chimpanzees displayed an appreciation of the common ground between themselves and their human interlocutors; however, we are reluctant to credit these animals (or even human infants) with such a sophisticated psychological appreciation on the basis simply of where they positioned themselves while communicating about desirable entities. We believe the present findings significantly undermine the validity of the measure of proximity in signaling as an index of the appreciation of common ground, in any species. However, there is ample room, at the present state of knowledge, and notwithstanding our skepticism, to argue that both the chimpanzees who signaled about food from a distance in the present study and the children who did so in van der Goot et al. (2014) were displaying their appreciation of a common ground. In short either (a) van der Goot et al. (2014) have correctly identified a behavioral index of the appreciation of a common ground and our findings demonstrate that this capacity is also evinced by chimpanzees, or (b) the proximity of signaling is not a valid index of the appreciation of the state of common ground in any species.

For van der Goot et al. (2014; and see related arguments by Povinelli & Eddy, 1996; Tomasello, Carpenter, & Liszkowski, 2007) it is the fact of the differences in response patterns between humans and apes that they claim supports their interpretation of psychological differences between humans and apes in these simple experimental protocols. What our data demonstrate, with larger samples, is that there is no empirical, behavioral basis to support the claim that great apes and young humans differ in psychological responses to these kinds of simple challenge. Importantly, in our view, neither van der Goot et al. (2014) nor the present study can directly address questions about the mechanisms supporting hidden, hypothetical psychological processes, because all we measured was overt communicative and locomotor

behavior, and we did not manipulate response outcomes for the subjects. Virtually all animals communicate and locomote, and there is no apparent reason to believe that merely documenting the confluence of these activities in humans or nonhumans will give us any special insight as to the cognitive processes involved—to accomplish this, at the very least, the subjects would need to be subjected to an assessment of their discriminative capacities in the face of differential response outcomes, a technique not employed either here or by van der Goot et al. (2014).

There is an additional concern that we would like to raise about the nature of species comparisons. There are several contemporary practices that, we believe, are seriously hampering theoretical development in the area of comparative-developmental evolutionary psychology. The first problem is that of overgeneralization from small samples. As demonstrated by the present study, van der Goot et al. (2014) overgeneralized from their particular sample of zoo-housed apes to all apes, everywhere. Their theoretical interpretation of the absence of distal communication in their sample requires that their subjects are representative of their species (chimpanzees and bonobos). As Figure 2 makes abundantly clear, in fact, their ape subjects' response patterns are not at all typical of captive apes; in fact, their apes behaved in an extremely unusual manner. To be clear, we have no objection to small-sample studies—what we object to is the repeated failure by practitioners to appreciate that findings in short, small-subject studies ought not to be taken as representative of the species, until confirmed with additional study. Of course, van der Goot et al. (2014) are not alone in overgeneralizing from their samples. For example, Povinelli and his colleagues (e.g., Povinelli & Eddy, 1996; Reaux, Theall, & Povinelli, 1999) claimed that chimpanzees were oblivious to the direction of human eyes, but Hostetter, Russell, Freeman, & Hopkins (2007) found that similarly institutionally housed chimpanzees had no systematic difficulty discerning human eye orientations and visibility, when they were simply

allowed to choose their own responses to differentially manipulated experimenters' gaze directions, and many similar refutations exist in the literature.

False negative findings in great apes have been widely promulgated when unrepresentative findings were overgeneralized, and when human and ape samples were not age-matched, or matched on critical rearing experience variables. These false negatives can have a disproportionate effect on theory construction in the study of human and non-human socio-cognitive development. Particularly in an age in which we have unprecedented capacities to sample brain morphology and function *in vivo* and rapidly developing capacities for genomic sequencing, our discipline is vulnerable to amplified effects of false premises. For example, there is a widespread assumption that humans have unique capacities for understanding gaze or pointing or other deictic cues, which has been refuted by simple reviews of the existing literature (Leavens, 2014, Lyn, 2010; Mulcahy & Hedge, 2012). Some have argued that humans have uniquely collaborative motivations or unique capacities to form common ground with others even before they can speak, but this is significantly challenged by the findings of Volter, Rossano, & Call, 2015. Again, it has been argued that humans have unique capacities to communicate about absent entities, which was refuted by Lyn et al., 2014, and, indeed, falsified in advance by virtually all of the ape language training studies since Kellogg & Kellogg, 1933. Finally, it has been argued that humans have unique capacities for imitation (refuted by Custance, Whiten, & Bard, 1995; Whiten et al., 1996). The danger is that neuroscientists and geneticists will squander significant time and other resources attempting to find the neural or genetic correlates of these false species differences; because numerous, systematic differences do exist between humans and our nearest living relatives in genomes and brain anatomy and function, these will be false associations attributable to false premises. We believe that the

solution lies in providing sufficient training to display the capacity in question; if an organism lacks an ability, then no amount of training will inculcate that ability. If a learning pathway exists to a competency, then it is invalid to argue that the species in question lacks that competency. In sum, having well-defined, documented phenotypes that are not subject to change with simple variations in methodology will provide a much more powerful framework for scientists interested in the genetic and neural basis of human cognitive specializations.

Finally, we think it is important to recognize that institutionalized apes, like those studied by van der Goot et al. (2014) and ourselves, necessarily live in the least complex social and physical environments of all apes, particularly in comparison to apes born and raised in the wild or to apes who have been raised as part of a human family-like environment (e.g., Bard & Leavens, 2009, 2014; Boesch, 2012; Kellogg & Kellogg, 1933; Leavens & Bard, 2011; Lyn, 2010). Nevertheless, institutional environments do pose unique ecological challenges. In particular, the physical circumstance of barriers to direct grasping of objects poses what we term the Referential Problem Space (Leavens, Hopkins, & Bard, 2005a); a repeated circumstance in which one organism is dependent upon another organism to act upon the world for them. These kinds of circumstances are exceedingly rare in wild habitats, but when these rare circumstances do occur, apparently deictic behavior is displayed by wild chimpanzees, at a distance, and with no intervening physical barriers (e.g., when one animal is dominating a food source, see Hobaiter, Leavens, & Byrne, 2014). Thus, we interpret apes' communication about distal entities as part of a general tactic of social manipulation that is also displayed by human children who spend enormous amounts of time in conditions of physical restraint (e.g., in car seats, cribs, cots, backpacks, feeding chairs, and so on), leaving them reliant upon others to act on the world for them (Leavens et al., 2005a). Because tactics of manipulation with deictic signals emerge in

these kinds of circumstances in both humans and apes, we believe that there is no evidence-based rationale to conclude either that (a) humans have unique cognitive capacities to support their deictic signaling or (b) that deictic signaling is, necessarily, a cognitively advanced ability. There may be, however, uniquely human cognitive processes associated with distal pointing, as argued by Tomsello et al. (2007), Liebal, Behne, Carpenter, & Tomasello (2009), and van der Goot et al. (2014), among others; our argument is that the mere fact of distal pointing does not constitute evidence for a human-unique cognitive ability, given that apes also communicate triadically and distally in captivity (e.g., Leavens & Hopkins, 1998; Savage-Rumbaugh, Rumbaugh, & McDonald, 1985; the present study) and in the wild (Hobaiter et al., 2014; Veà & Sabater-Pi, 1998). A potentially fruitful future direction in this line of investigation (kindly suggested to us by an anonymous reviewer) would involve replications with apes of the protocols used by researchers with human infants to demonstrate infants' discrimination of different degrees of shared experience with others. For example, Liebal et al. (2009) demonstrated that 18-month-old human infants responded appropriately to experimenters' pointing gestures in accordance with the nature of the shared activities the children had had with those experimenters. It remains an open question whether great apes would similarly discriminate between people based on their different shared activities.

In conclusion, the present findings unambiguously refute claims to the effect that great apes do not communicate about entities from a distance. Either chimpanzees possess the same appreciation for a state of common ground with experimenters that van der Goot et al. (2014) claimed for their human 12-month-olds (i.e., this is a shared capacity of humans and chimpanzees), or—we think more likely— proximity of signaling does not index this appreciation.

References

- Bakeman, R., & Quera, V. (2011). *Sequential analysis and observational methods for the behavioral sciences*. Cambridge: Cambridge University Press.
<http://dx.doi.org/10.1017/CBO9781139017343>
- Bard, K. A. (1992). Intentional behavior and intentional communication in young free-ranging orangutans. *Child Development*, 62, 1186-1197. <http://dx.doi.org/10.2307/1131526>
- Bard, K. A., & Leavens, D. A. (2009). Socio-emotional factors in the development of joint attention in human and ape infants. In L. Röska-Hardy & E. M. Neumann-Held (Eds.), *Learning from animals? Examining the nature of human uniqueness* (pp. 89-104). London: Psychology Press. <http://dx.doi.org/10.1891/1945-8959.10.1.9>
- Bard, K. A., & Leavens, D. A. (2014). The importance of development for comparative primatology. *Annual Review of Anthropology*, 43, 183-200.
<http://dx.doi.org/10.1146/annurev-anthro-102313-030223>
- Bard, K. A., Bakeman, R., Boysen, S. T., & Leavens, D. A. (2014). Emotional engagements predict and enhance social cognition in young chimpanzees. *Developmental Science*, 17, 682-696. <http://dx.doi.org/10.1111/desc.12145>
- Bates, E., Benigni, L., Bretherton, I., Camaioni, L., & Volterra, V. (1977). From gesture to the first word. In I. M. Lewis & L. Rosenblum (Eds.), *Interaction, conversation and the development of language* (pp. 247-308). New York: Wiley.
- Boesch, C. (2007). What makes us human *Homo sapiens*? The challenge of cognitive cross-species comparison. *Journal of Comparative Psychology*, 121, 227-240.
<http://dx.doi.org/10.1037/0735-7036.121.3.227>
- Boesch, C. (2012). *Wild cultures: A comparison between chimpanzee and human cultures*.

- Cambridge: Cambridge University Press. <http://dx.doi.org/10.1017/cbo9781139178532>
- Burkart, J. M., Hrdy, S. B., & van Schaik, C. P. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, 18, 175-186.
<http://dx.doi.org/10.1002/evan.20222>
- Carpenter, M. & Call, J. (2013). How joint is the joint attention of apes and human infants? In J. Metcalfe & H. S. Terrace (Eds.), *Agency and joint attention* (pp. 49-61). New York: Oxford University Press. <http://dx.doi.org/10.1093/acprof:oso/9780199988341.003.0003>
- Carpenter, M., Tomasello, M., Savage-Rumbaugh, S. (1995). Joint attention and imitative learning in children, chimpanzees, and enculturated chimpanzees. *Social Development*, 4, 217-237. <http://dx.doi.org/10.1111/j.1467-9507.1995.tb00063.x>
- Custance, D. M., Whiten, A., & Bard, K. A. (1995). Can young chimpanzees (*Pan troglodytes*) imitate arbitrary actions? Hayes & Hayes (1952) revisited. *Behaviour*, 132, 837-859.
<http://dx.doi.org/10.1163/156853995x00036>
- Desrochers, S., Morissette, P., & Ricard, M. (1995). Two perspectives on pointing in infancy. In C. Moore & P. J. Dunham (Eds.), *Joint attention: Its origins and role in development* (pp. 85-101). Hillsdale, N.J.: Lawrence Erlbaum Associates.
- Fox, N. A., Henderson, H. A., Marshall, P. J., Nichols, K. E., & Ghera, M. M. (2005). Behavioral inhibition: Linking biology and behavior within a developmental framework. *Annual Review of Psychology*, 56, 235-262.
<http://dx.doi.org/10.1146/annurev.psych.55.090902.141532>
- Franco, F., & Butterworth, G. (1996). Pointing and social awareness: Declaring and requesting in the second year. *Journal of Child Language*, 23, 307-336.
<http://dx.doi.org/10.1017/s0305000900008813>

- Froese, T., & Leavens, D. A. (2014). The direct perception hypothesis: Perceiving the intention of another's action hinders its precise imitation. *Frontiers in Psychology*, 5(65), 1-15. <http://dx.doi.org/10.3389/fpsyg.2014.00065>
- Garcia Coll, C., Kagan, J., & Reznick, J. S. (1984). Behavioral inhibition in young children. *Child Development*, 55, 1005-1019. <http://dx.doi.org/10.2307/1130152>
- Herrmann, E., Call, J., Hernandez-Lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans have evolved specialized skills of social cognition: The cultural intelligence hypothesis. *Science* 317, 1360–1366. <http://dx.doi.org/10.1126/science.1146282>
- Hobaiter, C., Leavens, D. A., & Byrne, R. W. (2014). Deictic gesturing in wild chimpanzees? Some possible cases. *Journal of Comparative Psychology*, 128, 82-87. <http://dx.doi.org/10.1037/a0033757>
- Hopkins, W. D., Russell, J. L., McIntyre, J., & Leavens, D. A. (2013). Are chimpanzees really so poor at understanding imperative pointing? Some new data and an alternative view of canine and ape social cognition. *PLoS ONE*, 8, e79338. <http://dx.doi.org/10.1371/journal.pone.0079338>
- Horowitz, A. C. (2003). Do humans ape? Or do apes human? Imitation and intention in humans (*Homo sapiens*) and other animals. *Journal of Comparative Psychology*, 117, 325–336. <http://dx.doi.org/10.1037/0735-7036.117.3.325>
- Hostetter, A. B., Russell, J. L., Freeman, H., & Hopkins, W. D. (2007). Now you see me, now you don't: Evidence that chimpanzees understand the role of the eyes in attention. *Animal Cognition*, 10, 55-62. <http://dx.doi.org/10.1007/s10071-006-0031-x>
- Kellogg, W. N., & Kellogg, L. A. (1933). *The ape and the child: a study of early environmental influence upon early behavior*. New York: McGraw-Hill.

Leavens, D. A. (2004). Manual deixis in apes and humans. *Interaction Studies*, 5, 387-408.

<http://dx.doi.org/10.1075/is.5.3.05lea> [Reprinted in C. Abry, A. Vilain, & J-L. Schwartz (Eds.), (2009). *Vocalize to localize*, pp. 67-86, Amsterdam: John Benjamins.

<http://dx.doi.org/10.1075/bct.13.06lea>]

Leavens, D. A. (2012). Pointing: Contexts and instrumentality. In S. Pika & K. Liebal (Eds.), *Current developments in primate gesture research* (pp. 181-197). Amsterdam: Benjamins.

Leavens, D. A. (2014). The plight of the sense-making ape. In M. Cappuccio & T. Froese (Eds.), *Enactive cognition at the edge of sense-making* (pp. 81-104). Basingstoke, U.K.: Palgrave Macmillan. <http://dx.doi.org/10.1057/9781137363367.0010>

Leavens, D. A., & Bard, K. A. (2011). Environmental influences on joint attention in great apes: Implications for human cognition. *Journal of Cognitive Education and Psychology*, 10, 9-31. <http://dx.doi.org/10.1891/1945-8959.10.1.9>

Leavens, D. A., & Hopkins, W. D. (1998). Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology*, 34, 813-822. <http://dx.doi.org/10.1037//0012-1649.34.5.813>

Leavens, D. A., & Hopkins, W. D. (2005). Multimodal concomitants of manual gesture by chimpanzees: Influence of food size and distance. *Gesture*, 5, 73-88. <http://dx.doi.org/10.1075/gest.5.1.07lea> [Reprinted in K. Liebal, C. Muller, & S. Pika (Eds.), (2007). *Gestural communication in nonhuman and human primates* (pp. 67-80). Amsterdam: John Benjamins. <http://dx.doi.org/10.1075/bct.10.07lea>]

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110, 346-353.

<http://dx.doi.org/10.1037//0735-7036.110.4.346>

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005a). Understanding the point of chimpanzee pointing: Epigenesis and ecological validity. *Current Directions in Psychological Science*, *14*, 185-189. <http://dx.doi.org/10.1111/j.0963-7214.2005.00361.x>

Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2008). The heterochronic origins of explicit reference. In J. Zlatev, T. Racine, C. Sinha, & E. Itkonen (Eds.), *The shared mind: Perspectives on intersubjectivity* (pp. 187-214). Amsterdam: John Benjamins.

<http://dx.doi.org/10.1075/celcr.12.12lea>

Leavens, D. A., Hopkins, W. D., & Thomas, R. K. (2004). Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *118*, 48-57.

<http://dx.doi.org/10.1037/0735-7036.118.1.48>

Leavens, D. A., Russell, J. L., & Hopkins, W. D. (2005b). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development*, *76*, 291-306. <http://dx.doi.org/10.1111/j.1467-8624.2005.00845.x>

Lempers, J. D. (1979). Young children's production and comprehension of nonverbal deictic behaviors. *The Journal of Genetic Psychology*, *135*, 93-102.

<http://dx.doi.org/10.1080/00221325.1979.10533420>

Liszkowski, U., Schäfer, M., Carpenter, M., & Tomasello, M. (2009). Prelinguistic infants, but not chimpanzees, communicate about absent entities. *Psychological Science*, *20*(5), 654-660. <http://dx.doi.org/10.1111/j.1467-9280.2009.02346.x>

Lyn, H. (2010). Environment, methodology, and the object choice task in apes: evidence for declarative comprehension and implications for the evolution of language. *Journal of Evolutionary Psychology*, *8*, 333-349. <http://dx.doi.org/10.1556/jep.8.2010.4.3>

- Lyn, H., Russell, J. L., Leavens, D. A., Bard, K. A., Boysen, S. T., Schaeffer, J., & Hopkins, W. D. (2014). Apes communicate about absent and displaced objects: Methodology matters. *Animal Cognition*, *17*, 85-94. <http://dx.doi.org/10.1007/s10071-013-0640-0>
- Mulcahy, N. J., & Hedge, V. (2012). Are great apes tested with an object object-choice task? *Animal Behaviour*, *83*, 313–321. <http://dx.doi.org/10.1016/j.anbehav.2011.11.019>
- Mundy, P., Kasari, C., & Sigman, M. (1992). Nonverbal communication, affective sharing, and intersubjectivity. *Infant Behavior and Development*, *15*, 377-381.
[http://dx.doi.org/10.1016/0163-6383\(92\)80006-g](http://dx.doi.org/10.1016/0163-6383(92)80006-g)
- Pedersen, J., Segerdahl, P., & Fields, W. M. (2009). Why apes point: Pointing gestures in spontaneous conversation of language-competent *Pan/Homo* bonobos. In E. Potocki & J. Krasinski (eds.), *Primateology: Theories, methods, and research* (pp. 53-74). Hauppauge, NY: Nova.
- Plooij, F. X. (1978). Some basic traits of language in wild chimpanzees? In A. Lock (Ed.), *Action, gesture and symbol* (pp. 111–131). London: Academic Press.
- Povinelli, D. J. & Eddy, T. J. (1996). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development*, *61*, 1-152.
<http://dx.doi.org/10.2307/1166159>
- Povinelli, D. J., Bierschwale, D. T., & Čech, C. G. (1999). Comprehension of seeing as a referential act in young children, but not juvenile chimpanzees. *British Journal of Developmental Psychology*, *17*, 37-60. <http://dx.doi.org/10.1348/026151099165140>
- Racine, T. P., Leavens, D. A., Susswein, N., & Wereha, T. J. (2008). Conceptual and methodological issues in the investigation of primate intersubjectivity. In F. Morganti, A. Carassa & G. Riva (Eds.), *Enacting intersubjectivity: A cognitive and social*

- perspective to the study of interactions* (pp. 65-79). Amsterdam: IOS Press.
- Reaux, J. E., Theall, L. A. & Povinelli, D. J. (1999). A longitudinal investigation of chimpanzees' understanding of visual perception. *Child Development*, 70, 275-290.
<http://dx.doi.org/10.1111/1467-8624.00021>
- Russell, J. L., Lyn, H., Schaeffer, J. A., & Hopkins, W. D. (2011). The role of socio-communicative rearing environments in the development of social and physical cognition in apes. *Developmental Science*, 14, 1459–1470. <http://dx.doi.org/10.1111/j.1467-7687.2011.01090.x>
- Savage-Rumbaugh, E. S., Rumbaugh, D. M., & McDonald, K. (1985). Language learning in two species of apes. *Neuroscience & Biobehavioral Reviews*, 9, 653-665.
[http://dx.doi.org/10.1016/0149-7634\(85\)90012-0](http://dx.doi.org/10.1016/0149-7634(85)90012-0)
- Thomas, E., Murphy, M., Pitt, R., Rivers, A., & Leavens, D. A. (2008). Understanding of visual attention by adult humans (*Homo sapiens*): A partial replication of Povinelli, Bierschwale, and Čech (1999). *Journal of Comparative Psychology*, 122, 428-436.
<http://dx.doi.org/10.1037/0735-7036.122.4.428>
- Tomasello, M. (1995). Joint attention as social cognition. In C. Moore & P. J. Dunham (Eds.), *Joint attention: Its origins and role in development* (pp. 103-130). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Tomasello, M. (2008). *Origins of human communication*. Cambridge, MA: The MIT Press.
- Tomasello, M., Call, J., & Gluckman, A. (1997). Comprehension of novel communicative signs by apes and human children. *Child Development*, 68, 1067-1080.
<http://dx.doi.org/10.2307/1132292>
- Tomasello, M., Carpenter, M., & Liszkowski, U. (2007). A new look at infant pointing. *Child*

- Development*, 78, 705–722. <http://dx.doi.org/10.1111/j.1467-8624.2007.01025.x>
- van der Goot, M. H., Tomasello, M., & Liszkowski, U. (2014). Differences in the nonverbal requests of Great Apes and human infants. *Child Development*, 85, 444-455.
<http://dx.doi.org/10.1111/cdev.12141>
- Veà, J. J., & Sabater-Pi, J. (1998). Spontaneous pointing behaviour in the wild pygmy chimpanzee (*Pan paniscus*). *Folia Primatologica*, 69, 289–290.
<http://dx.doi.org/10.1159/000021640>
- Volter, C. J., Rossano, F., & Call, J. (2015). From exploitation to cooperation: social tool use in orang-utan mother-offspring dyads. *Animal Behaviour*, 100, 126-134.
<http://dx.doi.org/10.1016/j.anbehav.2014.11.025>
- Whiten, A., Custance, D. M., Gómez, J.- C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110, 3–14.
<http://dx.doi.org/10.1037//0735-7036.110.1.3>

Table 1

Number of Chimpanzees with IJA Responses by Rearing History, Sex, and Number of Trials

	Number of Correct IJA Responses					Percent Correct
	0	1	2	3	4	

<i>Rearing</i>						
Mother (<i>n</i> = 90)						
<i>Female</i> (<i>n</i> = 56)	14	12	9	8	13	47.3
<i>Male</i> (<i>n</i> = 34)	7	7	5	6	9	52.2
Nursery (<i>n</i> = 39)						
<i>Female</i> (<i>n</i> = 23)	4	1	3	7	8	62.3
<i>Male</i> (<i>n</i> = 16)	2	3	3	3	5	59.4
Wild (<i>n</i> = 37)						
<i>Female</i> (<i>n</i> = 24)	4	3	6	2	9	59.4
<i>Male</i> (<i>n</i> = 13)	1	3	3	0	6	63.5
<i>Overall</i> (<i>N</i> = 166)	32	29	29	26	50	57.8

(table continues)

Notes. IJA = initiation of joint attention. Percent Correct = (the number of correct trials divided by the total number of trials [4]) * 100. For each row, the number of subjects is the total number of trials from which the percentages are derived.

Table 2

Number of Chimpanzees with TRI Responses by Rearing History, Sex, and Number of Trials

	Number of Correct TRI Responses					Percent Correct
	0	1	2	3	4	
<hr/>						
<i>Rearing</i>						
Mother (<i>n</i> = 90)						
<i>Female</i> (<i>n</i> = 56)	28	13	9	3	3	23.2
<i>Male</i> (<i>n</i> = 34)	16	8	1	4	5	30.9
Nursery (<i>n</i> = 39)						
<i>Female</i> (<i>n</i> = 23)	7	4	6	6	0	37.0
<i>Male</i> (<i>n</i> = 16)	6	4	2	2	2	34.4
Wild (<i>n</i> = 37)						
<i>Female</i> (<i>n</i> = 24)	12	4	4	1	3	28.1
<i>Male</i> (<i>n</i> = 13)	5	4	0	1	3	36.5
<i>Overall</i> (<i>N</i> = 166)	74	37	22	17	16	31.7

(table continues)

Notes. TRI = triangulated signaling. Percent Correct = (the number of correct trials divided by the total number of trials [4]) * 100. For each row, the number of subjects is the total number of trials from which the percentages are derived.

Table 3

Frequencies (and percents) of Communicative Acts by Type (N = 166)

	Trial No.			
	1	2	3	4
No communication	84 (51)	68 (41)	75 (45)	74 (45)
Gesture to Food (Pointing)	32 (19)	38 (23)	43 (26)	48 (29)
Gesture to Experim.	37 (22)	45 (27)	33 (20)	30 (18)
Other	13 (8)	15 (9)	15 (9)	14 (8)

Notes. "No communication" includes apparent lack of signaling, exhibitions of parts of the body, plus apparent signals not accompanied by gaze alternation. "Other" includes cage bangs, bartering attempts, spitting, and throwing. Percentages may not sum to 100, due to rounding error.

Figure Captions

Figure 1. The positional behavior of the chimpanzees as the percent of subjects who (a) approached the food and communicated with the experimenter (Food); (b) positioned themselves between the food and the experimenter and communicated about the food with the experimenter (Middle), and (c) approached the experimenter and communicated about the food with the experimenter (Exper.). “Exper.” = experimenter. Sample sizes refer to the number of individuals who signaled out of the total sample of 166 chimpanzees.

Figure 2. The percent of subjects who communicated from a position proximal to the food (Proximal) and the percent of apes who communicated from a position distal to the food (Distal) in the present study (Trials 1-4, chimpanzees at UTMDACC and YNPRC). Babies 1 and Babies 2 refer to the human infants in van der Goot et al. (2013), their Experiments 1 and 3, respectively. The last group on the right are the apes in the original study at the Leipzig Zoo by van der Goot et al. (2014; Leip. Apes). Chimpanzees who communicated from the Middle or near the Experimenter were combined and categorized as Distal communicators for the purposes of this comparison. Sample sizes refer to the number of individuals who signaled out of the total sample of 166 chimpanzees (left to right, the first four trials from the present study comprising chimpanzees from UTMDACC and YNPRC), the total number of babies (Babies 1 and Babies 2) who signaled or locomoted in Experiments 1 and 3, respectively, from van der Goot et al. (2014), and, in the last group, the apes at Leipzig Zoo, from van der Goot et al. (2014). Statements about significance are from the respective studies (UTMDACC and YNPRC chimpanzees, Trials 1-4 from the present study, Babies 1, Babies 2, and Leip. Apes from van der Goot et al., 2014); data for the last three groups from van der Goot et al. (2014, their Figure 2). "NS" = not significantly different; "*" = $p < .05$.

Figure 1

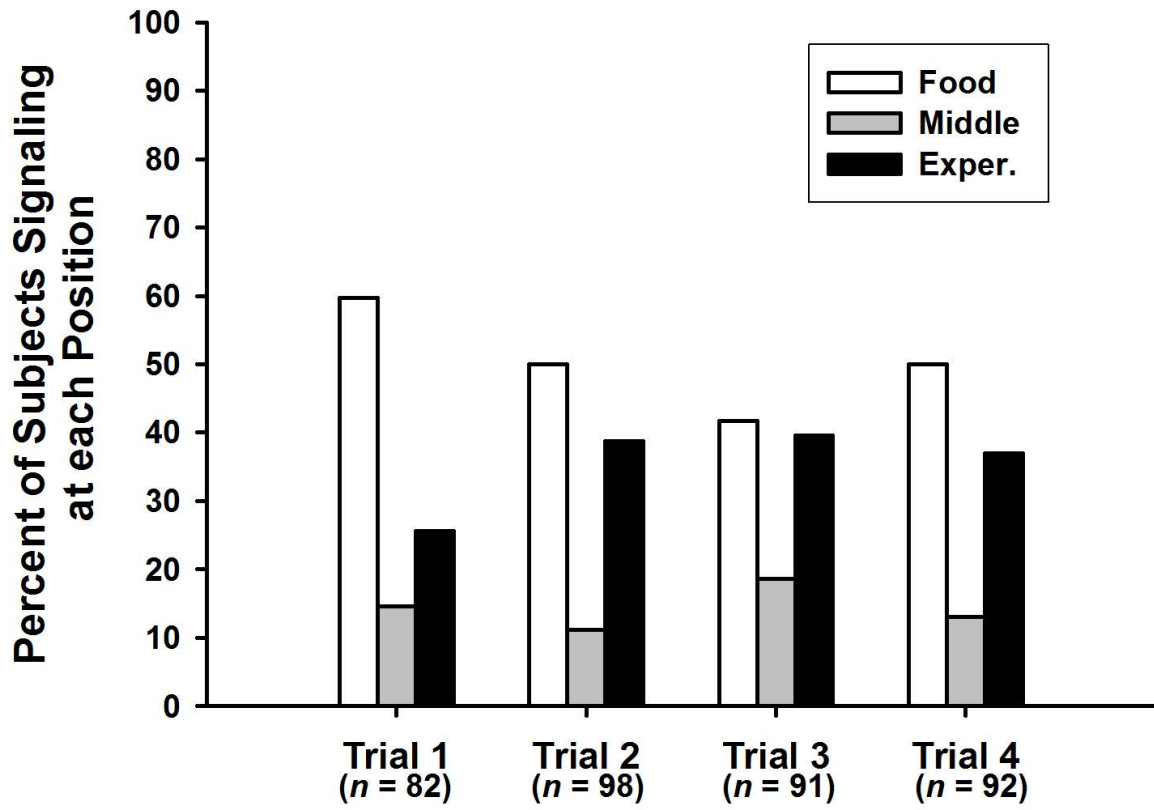


Figure 2

