



Bonobos point more for ignorant than knowledgeable social partners

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Numerous uniquely human phenomena, from teaching to our most complex forms of cooperation, depend on our ability to tailor our communication to the knowledge and ignorance states of our social partners. Despite four decades of research into the “theory of mind” capacities of nonhuman primates, there remains no evidence that primates can communicate on the basis of their mental state attributions, to enable feats of coordination. Moreover, recent reevaluation of the experimental literature has questioned whether primates can represent others’ ignorance at all. The present preregistered study investigated whether bonobos are capable of attributing knowledge or ignorance about the location of a hidden food reward to a cooperative human partner, and utilizing this attribution to modify their communicative behavior in the service of coordination. Bonobos could receive a reward that they had watched being hidden under one of several cups, if their human partner could locate the reward. If bonobos can represent a partner’s ignorance and are motivated to communicate based on this mental state attribution, they should point more frequently, and more quickly, to the hidden food’s location when their partner is ignorant about that location than when he is knowledgeable. Bonobos indeed flexibly adapted the frequency and speed of their communication to their partner’s mental state. These findings suggest that apes can represent (and act on) others’ ignorance in some form, strategically and appropriately communicating to effectively coordinate with an ignorant partner and change his behavior.

social cognition | theory of mind | coordination | primates | communication

A growing body of work suggests that monkeys and apes share with humans rich precursors of theory of mind, the ability to infer the mental states that guide others’ actions (1–3). However, major debates concern what distinguishes human theory of mind in terms of both its functions and its underlying representations. Regarding function, various scholars have argued for decades that what makes humans special is a remarkable propensity for cooperation and that the underlying mechanism is a unique capacity to harness theory of mind to communicate in service of coordination (4). For example, we readily adapt our communication to the knowledge and ignorance states of our partners to change their mental states (5), and behavior, and enable cooperative acquisition of goals. While no research has addressed this ability in nonhuman great apes, two studies shed light on its precursors. First, Grueneisen et al. (6) found that chimpanzees and bonobos can facilitate coordination by adjusting the visibility of their actions for a cooperative partner relative to a competitive one, though their task did not involve communication or experimentally isolate theory of mind. Second, Crockford et al. (7) found that wild chimpanzees may be able to communicate based on a recipient’s mental state: Chimpanzees produced more warning vocalizations in the presence of groupmates who were ignorant about a nearby snake, compared to those who were knowledgeable. However, experiments in controlled and nonthreatening settings are needed to eliminate alternative explanations (e.g., that chimpanzees simply responded to others’ behavior, or were driven by arousal) and to clarify whether this capacity can be deployed flexibly in other contexts and via other communicative modalities. Paradigms with greater control are also essential for isolating the particular cues subjects are sensitive to and constraining the hypotheses about the underlying mechanisms driving this pattern of communication, especially following contradictory findings in captivity (8).

Regarding the underlying representations, a reevaluation of the literature has compellingly shown that controlled studies testing primates’ capacity to represent others’ knowledge or ignorance could be explained by attributing only knowledge-like states called awareness relations (9). This is because past paradigms make positive predictions only about how subjects should act if they have attributed knowledge (e.g., avoid food known to a competitor) but not ignorance (i.e., refs. 1, 3, and 10–12). Thus, no controlled studies have directly tested for primates’ capacity to represent others’ ignorance. One central

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prediction that distinguishes ignorance representation from deflationary accounts is that *only* primates who can represent others' ignorance should be able to act on those representations, for example, through communication.

To clarify the unique functions and representations underlying human theory of mind, we tested whether our closest relatives, bonobos (*Pan paniscus*), can identify a partner's ignorance and adapt communication to enable coordination. In a highly controlled preregistered study, captive bonobos could point and remedy a partner's ignorance. Bonobos could receive a reward that they had watched being hidden under one of several cups, if their human partner could locate the reward. If bonobos can represent a partner's ignorance and are motivated to communicate based on this mental state attribution, they should point more frequently, and more quickly, to the hidden food's location when their partner is ignorant about that location than when he is knowledgeable.

Results

Three male bonobos (Nyota, age 25; Kanzi, age 43; Teco, 13) participated in this preregistered experiment (<https://aspredicted.org/pfqk-2q4y.pdf>). A human experimenter (E1) sat opposite the subject at a sliding table with three overturned cups (Fig. 1). A second experimenter (E2), sitting perpendicular to the pair, played the role of gamemaster, baiting one cup on each trial. Bonobos first passed two sessions each of familiarization 1 and familiarization 2 (12 trials/session). During familiarization trials, both bonobo and E1 witnessed the baiting of a food item; E1 then revealed the food item either immediately (familiarization 1) or after a five second delay (familiarization 2) and E2 provided it to the bonobo. Familiarization sessions established a cooperative context between the bonobo and E1 (that E1 always revealed the hidden food when they knew its location) while reducing baseline pointing rates. Following familiarization, bonobos then completed eight test sessions of 15 trials. Each test session included three ignorance trials and three knowledge trials, embedded among nine familiarization 1 trials. Ignorance and knowledge trials were identical to familiarization trials in all ways but two. First, a barrier was placed between E1 and the cups during baiting. This barrier was opaque in the ignorance condition but had a viewing window in the knowledge condition (Fig. 1 *A* and *B*). Second, following baiting and the barrier's removal, E1 waited 10 s before responding (regardless of bonobo pointing), during which time he twice scanned the options and said "Hmm, where is the [item]?" Subjects could point to inform E1 of the food's location, and we recorded whether (1/0) and how quickly they did so. The critical prediction was that bonobos would point more frequently and/or more quickly, when their partner was ignorant than knowledgeable.

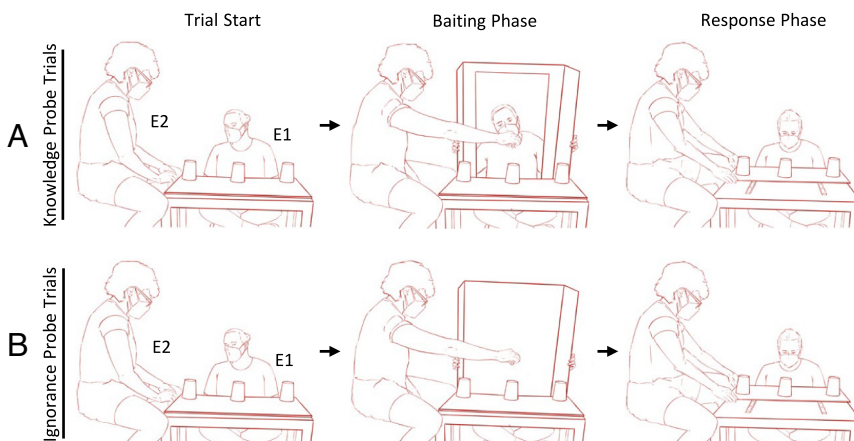


Fig. 1. Experimental setup during knowledge and ignorance trials from the bonobo's perspective. E1 observed baiting through a viewing window in Knowledge (A) but not Ignorance trials (B). Whether and how fast the bonobo spontaneously pointed for their Knowledgeable or Ignorant partner was recorded in a 10 s response window.

Logistic (point occurrence) and linear (point latency) regression models confirmed these predictions (Fig. 2 *A* and *B*; Open Science Framework (OSF) Appendix Tables S1–S8). Bonobos were significantly more likely to point ($\chi^2(1) = -1.236, P = 0.004, OR = 0.29, 95\%CI [0.12, 0.67]$) and did so significantly more quickly ($\chi^2(1) = 1.532, P = 0.005, \beta = 1.51, 95\%CI [1.13, 2.02]$) in ignorance trials than knowledge trials. Notably, when subjects did point, their accuracy was significantly above chance, for both ignorance and knowledge trials (P -values < 0.001 ; *SI Appendix*). This suggests that they concurrently held in mind not only E1's perspective, which in the case of ignorance was decoupled from reality, but also maintained an accurate, *separate* representation of reality. Finally, to confirm that pointing was not simply reaching and was indeed communicative, we conducted a control experiment with Nyota to test whether pointing depended on the presence of a communicative partner (*SI Appendix*). Critically, Nyota pointed significantly more for an ignorant experimenter than for no experimenter (Fig. 2C; OSF *SI Appendix*, Tables S15–S17).

Discussion

Challenging simpler representational accounts (e.g., the awareness relations account, 9), these findings suggest that bonobos are not only capable of representing another's ignorance (13, 14) but can act on these representations to effectively communicate and coordinate with another agent. Low familiarization pointing rates make clear that pointing to ignorant partners does not reflect high default pointing that is attenuated (in the knowledge condition) when the partner's knowledge or awareness is detected (OSF *SI Appendix*, Table S9). We also find no evidence for learning (OSF *SI Appendix*, Tables S10–S13). In contrast to Tauzin et al. (8), we show here that apes who are proficient in pointing *can* consider others' mental states to inform imperative pointing, under appropriate familiarization and experimental conditions (e.g., a cooperative context in which an informed experimenter will attempt to help, unlike typical object-choice contexts in which experimenters are usually knowledgeable and all that matters for obtaining food is whether apes point clearly). Our findings align with those of Crockford et al. (7) who showed that chimpanzees direct warning vocalizations toward ignorant groupmates but, critically, our design carefully eliminates arousal and partner behavior as potential explanations and isolates partner attention to baiting as the only differential social cue available for mind-reading (or behavior-reading). In concert with Crockford's work, our results suggest that apes possess a flexible ability to use theory of mind for communication and coordination, that is neither modality- nor context-specific. High point accuracy across both conditions suggests that bonobos were able to act upon their own

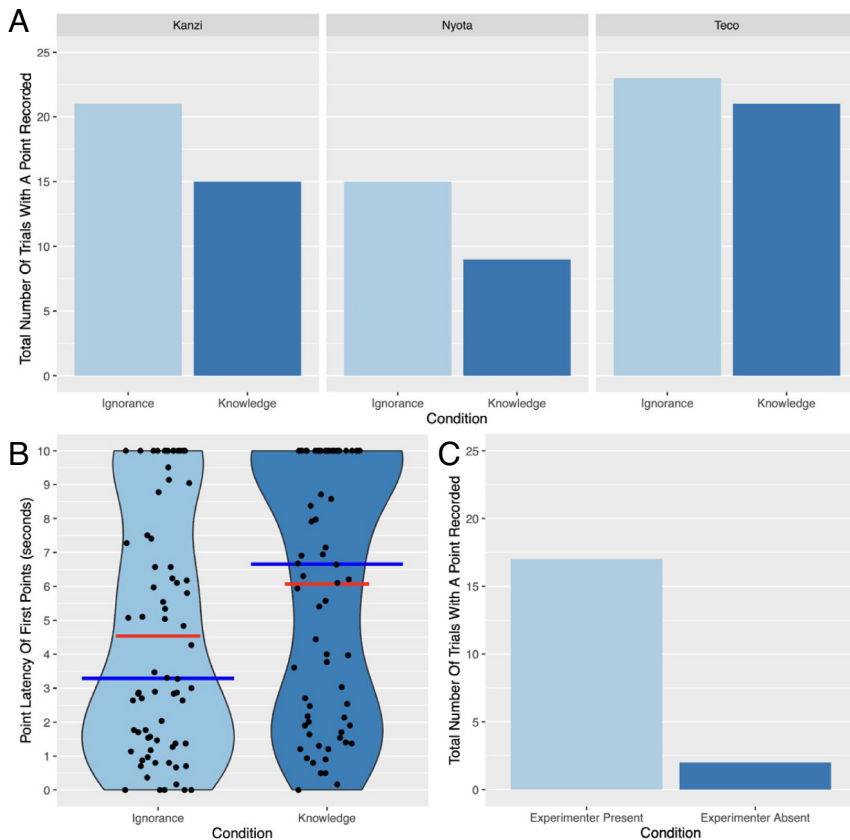


Fig. 2. Results. (A) Point occurrence per subject across 24 Knowledge and 24 Ignorance trials. (B) Group-level point latency. No-point trials recorded as maximum response time. Red and blue lines represent mean and median values, respectively. (C) Point occurrence in a control experiment with an ignorant communicative partner present vs. absent.

knowledge of the food's location, while also recognizing when the experimenter was in a state of ignorance. This suggests that apes are able to hold two conflicting representations in parallel (one that reflects the true nature of the world and another that does not), a finding crucial for establishing more advanced theory of mind cognition (14). These results challenge prominent accounts arguing that apes track others' epistemic states without any attention to their own knowledge of the situation (15). In our study, apes appear to point specifically because they identify a discrepancy between their partner's (lack of) knowledge and their own. A critical question for future research is whether apes use theory of mind with the goal of changing their partner's mental state or only their partner's behavior. In summary, we show that bonobos can represent ignorance in some form and harness these representations to communicate to change a cooperative partner's behavior. Some of the hallmark cognitive abilities that subserve uniquely human coordination and cooperation are within the cognitive potential of our closest relatives, and likely to be evolutionarily ancient.

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Materials and Methods

Supplementary methods appear in *SI Appendix*.

Ethical Note. Experimental protocols were approved by the Animal Care and Use Committees of both Johns Hopkins University and Ape Cognition and Conservation Initiative, and complied with international and institutional guidelines.

Data, Materials, and Software Availability. Raw data and analysis scripts are available as [supporting information](#). Supplementary tables, figures, results, and discussion, and other materials are available on the Open Science Framework (https://osf.io/em9ws/?view_only=ac5a2972d2a64f93ae94e9e8fd7c4c48) (16).

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